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The Provisioning Flights of Digger Wasps (Hymenoptera: Sphecidae) as a Defence against the Nest Parasite *Senotainia trilineata* (Diptera: Sarcophagidae)

by

D. B. McCorquodale

(C)

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SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

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Abstract

Digger wasps are subject to parasitism by several species of miltogrammine flies, the most important of which is the satellite fly, *Senotainia trilineata*. Many behaviours exhibited by female digger wasps are thought to act as deterrents to this parasite. One such behaviour is the flight during which female wasps return to their nests with prey. The pattern and characteristics of these provisioning flights vary greatly among species. They may function as a defence against satellite flies either by reducing the probability of detection, a primary defence, or by reducing the probability of larviposition once the flight is followed, a secondary defence.

Provisioning flights by females of six species of digger wasps (*Oxybelus uniglumis*, *Crabro argusinus*, *Bembix americana*, *Philanthus gibbosus*, *Philanthus inversus* and *Cerceris echo*) were observed for two summers at a nesting aggregation in southern Alberta. Responses of females to pursuit by satellite flies were recorded along with estimates of potential parasitism. The searching and larviposition behaviour of individually marked female *S. trilineata* were also observed to determine whether they were generalists or specialists in host selection.

No type of flight reduced the probability of detection by female *S. trilineata*. Provisioning flights by females of all six species were frequently and consistently followed. Female *S. trilineata* noticed and followed most moving

insects. Female *S. trilineata* were generalists in their searching behaviour.

The flights by females of two species (*Crabro argusinus* and *Philanthus inversus*) reduced the probability of larviposition once the wasp was followed by delaying the approach to the nest. In the other four species most females did not respond to the following fly and the fly frequently had an opportunity to larviposit on the prey. Some of these species have other defences against this nest parasite, such as progressive provisioning.

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Introduction

A striking feature of digger wasp nesting aggregations is the abundance and diversity of nest parasites. The most common and widespread nest parasites are sarcophagid flies in the subfamily Miltogramminae. The flies commonly destroy the wasp larvae in 10-20% of all cells provisioned by a wasp species (Evans 1970; Krombein *et al*. 1979) and in some aggregations more than 50% of the larva are destroyed (Kurczewski and Harris 1968; Evans 1958). In North America, one of the most abundant and widespread of the miltogrammines is the satellite fly, *Senotainia trilineata*. Females of this species frequent wasp nesting aggregations where they watch for and follow prey-laden female wasps to the entrance of their nests. In this vicinity they attempt to deposit one to several larvae on the wasp's prey. These larvae are then introduced into the nest when the wasp transports her prey to the cell she is provisioning. In the cell, the *S. trilineata* larvae consume the wasp's egg or the prey intended for the wasp larva. This usually results in the death of the wasp egg or larva in the parasitized cell. Sphecids of 6 subfamilies, as well as solitary ground nesting wasps of two other families (Vespidae and Pompilidae) have been recorded as hosts of this fly (Evans and Yoshimoto 1962; Kurahashi 1970; Krombein 1967; Krombein *et al*. 1979; Ristich 1956; Peckham 1977). The prevalence of parasitized cells for each wasp species varies greatly, but reports of more than 15% of all larvae of a

species being destroyed by *S. trilineata* are not uncommon (e.g. *Tachytes validus* 62.5%, Evans and Kurczewski 1966; *Oxybelus uniglumis* 33%, Evans 1970; *Crabro advena* 25%, Evans *et al.* 1980; *C. hilaris* 27%, Matthews *et al.* 1979; *Bicyrtes quadrifasciata* 20%, Evans 1966a). Since *S. trilineata* are so widespread, since they parasitize such a wide range of hosts and since parasitism is so prevalent in many species, they have been considered an important factor in shaping the life histories and behaviour patterns of many digger wasps (Evans 1966a, 1966b, 1970; Matthews and Matthews 1978; Alcock 1979).

An equally striking feature of digger wasp nesting aggregations is the set of species specific, stereotyped behaviour patterns each wasp uses to construct and provision her nest. As a result, each species is recognizable by a distinctive set of behaviour patterns. For example, in the genus *Oxybelus* the females of some species carry soil out of the nest with their mandibles and forelegs, whereas others rake the soil out with only their forelegs. The females of some species place temporary closures of sand over their nest entrances before they leave to hunt; others leave the entrance open. The females of some species carry their prey with their middle legs and others transport the prey on their sting (Peckham *et al.* 1973). Besides their obvious role in actually constructing and provisioning the nests, many of these behaviour patterns are thought to have a role in reducing the impact of miltogrammine nest parasites.

Temporary closures of the nest entrance may prevent hole searchers from finding the nest (Evans and Eberhard 1970), accessory burrows may deflect the attention of hole searchers from the real nest entrance (Tsuneki 1963; Evans 1966b) and carrying the prey tightly tucked under the thorax may reduce the accessibility of the prey to satellite flies (Evans 1963).

The pattern and speed of provisioning flights, like other behaviour patterns, are species specific and exhibit great diversity among species within a nesting aggregation (Evans 1970; Alcock 1973). During provisioning flights female *Ammophila procera* walk slowly to the nest, *Plenoculus davisi* employ short, direct hop flights, *Bicyrtes ventralis* fly quickly and directly to the nest entrance, *Philanthus crabroniformis* stop and sit a few times, and *Crabro argusinus* fly quickly toward the nest entrance, back away for a short distance, then quickly fly into the nest entrance (Evans 1959; Kurczewski 1968; Evans 1966a, 1970; Matthews *et al*. 1979). Within genera there is also much diversity in flight pattern. The genus *Philanthus* includes species whose females fly quickly and directly to the nest (*P. sanbornii*), descend slowly, waggling their abdomen conspicuously as they approach the nest (*P. gibbosus*), and fly slowly towards the nest, land and remain motionless, then slowly fly to the entrance (*P. inversus*)(pers. obs., see also Alcock 1975). As a result of this diversity, each species can be recognized by the distinctive provisioning

flight of its females in a multispecies nesting aggregation (Evans 1970, Alcock 1973, pers. obs.).

The obvious role of provisioning flights is to transport prey from the site of capture to the nest. Additionally, since satellite flies use vision to orient to wasps and follow them to their nests, flights might be involved in defence against this parasite (Evans 1970; Alcock 1973, 1974, 1975).

Edmunds (1974) broadly defines a defensive adaptation as an 'adaptation which reduces the chance of success of an attack by another animal'. Flight patterns may act as a defence by reducing the probability of a female *S. trilineata* following a provisioning wasp (a primary defence), or once a fly is following, by reducing the chance of a fly depositing a maggot on the prey carried by the wasp (a secondary defence). In this study a behaviour is considered a defence if it reduces the number of presumed larvipositions to below one per cell.

Provisioning Flights as a Primary Defence

Provisioning flights may act as a primary defence, reducing the probability of detection (Edmunds 1974), by the presentation of diverse flight types by each of several species in a nesting aggregation (Alcock 1973, 1974, 1975). The presentation of diverse forms, either morphological or behavioural, to a predator has been suggested to reduce the efficiency of a predator in subduing any one of the prey

forms (Ricklefs and O'Rourke 1975, Schall and Pianka 1980). The differences among species presumably require different skills for detection, resulting in the predator being differentially successful at finding each prey type. Several groups of animals are known to present diverse aspects, either morphological or behavioural, to their enemies (e.g. moths, Sargent 1978; Ricklefs and O'Rourke 1975; lizards, Schall and Pianka 1980; grasshoppers, Joern 1979). In a wasp nesting aggregation, Alcock (1973, 1974, 1975) reasons that an individual fly can effectively scan the environment for only some of the types of flights present and that each fly either is neurally programmed to receive visual stimuli only from certain flight patterns or responds selectively to only some of the types of flights it sees. Aspect diversity theory predicts, as Alcock suggests, that flight diversity would be selected for because each species would then escape detection by a portion of the satellite fly population.

Given that wasp provisioning flights are diverse, the hypothesis that flight diversity is involved in a primary defence against nest parasitism by *S. trilineata* can be evaluated by examining the behaviour of the satellite fly. If individual female *S. trilineata* notice and follow only one or a few types of provisioning flights aspect diversity may be a defence. Diversity may also be a defence if individuals follow the flights of many species, but each species at very different frequencies. If individual flies

frequently notice and follow many types of provisioning flights, then flight diversity is probably not involved in primary defence.

Provisioning Flights as a Secondary Defence

Once a satellite fly is following a provisioning wasp, the wasp may be able to use a flight pattern to respond to and deter the fly from larvipositing on her prey, a secondary defence (Edmunds1974). Two types of provisioning flights of sphecids have been reported to be secondary defences against satellite flies. Flights that lure the fly away from the nest are known for *Crabro argusinus* (Evans 1960; Matthews *et al.* 1979) and five species of *Philanthus* (*multimaculatus*, *crabroniformis*, *zebratus*, *lepidus* and *gibbosus*) (Evans 1970; Alcock 1975). Secondly, females of many of the same *Philanthus* (*multimaculatus*, *crabroniformis*, *zebratus* and *politus*) make stops on vegetation or the ground in the vicinity of their nests (Evans 1970; Alcock 1975). These have been interpreted as opportunities for the following *S. trilineata* to be distracted. Both Evans (1970) and Alcock (1974) have seen a satellite fly, which was watching a sitting wasp which it had previously been following, divert its attention from the sitting wasp to a wasp flying nearby. The effectiveness of these flights as defences is questionable because in the only quantitative data presented every cell was potentially provisioned with a prey contacted by a satellite fly (Alcock 1975).

Applying the aspect diversity hypothesis to escape behaviour, Schall and Pianka (1980) argue that diverse responses to a predator should reduce a predator's efficiency. For digger wasps, different responses by females of each species to a following *S. trilineata* could reduce the ability of the fly to predict and/or learn how each wasp species will react and therefore reduce larviposition efficiency. Alternatively, Alcock (1975) has predicted behavioural convergence on the one or few escape patterns that are effective.

Whether responses to satellite flies are diverse or have converged on one effective response can be determined by observing the reactions of several species of wasps to being followed and the effectiveness of the responses. Also, if individual *S. trilineata* specialize and are only able to contact prey during one type of wasp flight response, and different individuals vary in the response during which they are able to contact the prey, this would suggest that diverse responses reduce the probability of contact. Alternatively, if individual flies are able to contact prey during many types of responses and one response results in the prey rarely being contacted, convergence on one effective response has probably occurred.

Provisioning Flights not Involved in Defence

It is possible, however, that provisioning flights are not involved in defence against satellite flies. If many flights of a species are followed and no response is noted, it may be because other effective defences are being used, such as a defence taking place in the nest. Progressive provisioning in many bembicines is suggested to function in this manner (Evans 1957, 1966a).

To determine whether provisioning flights were effective primary or secondary defences, I monitored the flights of six species of digger wasps and the behaviour of *S. trilineata* at a nesting aggregation of wasps in southern Alberta. *S. trilineata* was common, and it followed and attempted to larviposit on the prey of all six wasp species. Frequencies of following and contact, and responses of wasps to being followed were recorded for each of the six species. Contacted prey were collected and nests were excavated to confirm the relationship between contact and actual introduction of *S. trilineata* larvae into nests.

Study Area and Methods

This study was conducted at Writing-on-Stone Provincial Park in southern Alberta (49° 06', 111° 20'), from May 21 to September 21, 1981 and from June 1 to September 19, 1982. The study site was a man-made sand scrape consisting of a 10 by 20 metre flat area of sand, sparsely vegetated with Russian Thistle (*Salsola kali*), sunflowers (*Helianthus* spp.) and several grasses, and an adjacent 1-2.5m vertical panel of hard-packed sand and gravel (Plate 1). The sand and gravel were derived from the nearby sandstone hoodoos and prairie. A few metres north of the scrape were southfacing sandstone cliffs, 8-10m high, which the vertical panel paralleled. Because of this the sand scrape held one of the warmest microclimates in the area. Surrounding shrubbery (*Prunus virginiana, Betula occidentalis*), grassy areas, sage (*Artemesia* spp.) flats and the nearby shoreline of the Milk River provided a diversity of microhabitats where female wasps hunted for arthropod prey.

This area of friable sand supported the largest and most diverse concentration of digger wasp nests in the vicinity. The six most common nesting species, *Oxybelus uniglumis* (Linnaeus), *Crabro argusinus* Bohart, *Bembix americana spinolae* Lepeletier, *Philanthus gibbosus* (Fabricius), *P. inversus* Patton and *Cerceris echo* Mickel were the subjects of this study. Nearby sandy river banks, graded roads and sandy bases of cliffs supported lower densities of nests of some of the species. Many other

species of sphecids also nested on the study site. Some of the more common or conspicuous ones were *Ammophila* spp., *Podalonia* spp., *Isodontia elegans*, *Diodontus* sp., *Miscophus* sp., *Plenoculus* sp., *Tachysphex* spp., *Tachytes* sp., *Larropsis* sp., *Ectemnius dilectus*, *Crossocerus* spp., *Bicyrtes ventralis*, *Hoplisoides placidus*, *Philanthus pulcher*, *P. psyche*, *P. sanbornii*, *Cerceris sexta* and *Eucerceris superba*.

Senotainia trilineata (Van der Wulp) was one of the two miltogrammine flies that were common throughout both summers. Only *S. trilineata* females followed provisioning wasps. *Phrosinella fulvicornis*, the most abundant miltogrammine, usually deposits its larvae in the temporary closures of nests of sphecids and does not follow provisioning females (Allen 1926; Evans 1970; Peckham 1977). Four other miltogrammines, *Hilarella hilarella*, *Euaraba tergata*, *Taxigramma heteroneura* and *Metopia argyrocephala* were observed fewer than ten times each during the study. Two other groups of hole-searching, hymenopteran nest parasites, mutillids (*Dasymutilla* spp.) and chrysidids were quite common. A few nest parasites of the sphecid genus *Nysson* were present infrequently.

Wasp and *S. trilineata* activity were monitored on almost every suitable day during the two summers, for a total of 375 hours in 1981 and 450 hours in 1982. Provisioning was frequent only when the air temperature was above 22°C, the winds were calm to moderate and clouds did

not obscure the sun. These conditions were met on about 70% of all days between June 20 and September 19 of both years. When conditions were not ideal some wasps were active, but provisioning was minimal. On most days a count of provisioning females of each wasp species and female *S. trilineata* was conducted. On some days the time of first activity, first provisioning, last provisioning and last activity of each species was noted.

Individual nests of the six species were marked with a numbered toothpick placed beside the entrance (Plate 2). Many of the female wasps associated with these nests were marked with an individually identifiable combination of Testor's Pla Enamel paint on the thorax (Table 1, Plate 3). The differences in numbers of individuals and nests marked reflect differences in effort devoted to each species between years rather than population changes, except where noted in the results. Each day as many active nests as possible were watched and all provisionings were recorded. Observation was most prevalent at nests close to *S. trilineata* activity. For the first ten provisionings and all those during which a *S. trilineata* followed the flight, I recorded the flight pattern in the last 0.5-5m, flight speed, height above sand, the presence of other wasps, *S. trilineata* or insects in a $4m^2$ area centred on the nest, time taken by the wasp to remove temporary closure (if present) and enter the nest, and type of prey carried. If a female *S. trilineata* followed the provisioning female during

her return to the nest, I recorded all the above details as well as the wasp's reaction to the fly and the fly's response to the wasp. From these data the frequencies of following and contact, and contact to followed ratio were calculated for each wasp species. Chi-square tests for goodness-of-fit were used to compare frequencies within and between years. Other statistical tests are referred to in the appropriate tables. Because flights by more than one individual sometimes happened simultaneously, all details were not recorded for each flight. Because of these missing data, and disturbances such as collecting prey during some flights and inadvertently disturbing a few *S. trilineata* females while they were following a wasp, the number of flights used for each analysis varies.

Female *S. trilineata* deposit first instar larvae on prey of provisioning wasps near the nest entrance or as they enter the nest (Ristich 1956; Peckham 1977). Contact with the prey of the wasp was considered to have occurred if 1) direct contact of the fly's abdomen with the prey was observed, 2) the fly jumped onto the wasp with prey or 3) the fly entered the nest entrance with the wasp and her prey. Contact does not necessarily mean larviposition on the prey, but larviposition requires contact. To determine the relationship between contact and larvipositon several contacted prey of *P. gibbosus* and *C. argusinus* were collected and examined for signs of *S. trilineata* maggots immediately after contact, and then periodically for ten

days. Prey items were also collected at the nest entrances for identification and to determine if any prey which were not followed or contacted harboured maggots.

The number of contacts per cell were calculated for each species assuming a random distribution of contacted prey and that each cell contained the mean number of prey for the species. These numbers are meant to be comparative, not to represent actual rates of parasitism. A contact is a necessary prerequisite for a larviposition and nest parasitism by *S. trilineata*. Therefore this measure should correlate well with rates of parasitism only if the species in question employs no post-larviposition defences against *S. trilineata*.

Nests of *Oxybelus uniglumis*, *Crabro argusinus*, *Bembix americana* and *Cerceris echo* were excavated to determine prevalence of maggots, number of cells per nest and number of prey per cell. Nest excavation was minimized to avoid excessive damage to other nests in the small sand scrape. For this reason nests of *B. americana* and *C. echo* from a sandy area 8km away were also excavated.

Many satellite flies were also individually marked with Testor's paints (Table 1, Plate 4). In 1982 44 marked flies were continuously observed for 1-30 minutes to record their reactions to moving objects. All insects moving through a 0.5m² field of view in front of the fly were recorded along with the response of the fly to them. Small pebbles were tossed 10-30cm in front of many of these flies (N=30) and

their responses to the pebbles were recorded. Responses were scored on a scale of 0 to 5: 0-No response, 1-Orient toward, 2-Fly at, 3-Short follow(<1m), 4-Long follow(>1m), 5-Attempt to contact. For some analyses, categories 0 and 1 were lumped as no approach, 3 and 4 as follow and 3-5 as an approach.

Voucher specimens of the six wasp species, their prey and *S. trilineata* have been deposited with the Department of Entomology, University of Alberta and the Canadian National Collection, Biosystematics Research Institute, Ottawa.

Results

Behaviour of *Senotainia trilineata*

Female *Senotainia trilineata* were active throughout the summer of 1981 (May 21 until September 19). At times several females were present each day for several days, at other times several days would pass without sightings of females. The flies were most common in late June, throughout July and in early September. In 1982 the first female was not seen until June 20. Throughout July and August, 8-14 females were present on most days that wasps provisioned (Fig. 1). In September numbers gradually declined; the last two flies were seen on September 18. In 1982 more female *S. trilineata* were present and the numbers were more stable than in 1981.

S. trilineata were generally active by the time most wasps started to provision in the morning and often before the first wasp provisioned (Table 2). Throughout the day a variable number were present; sometimes none, sometimes several. Numbers present in the sand scrape did not appear to correlate with wasp activity during the warm part of the day. Frequently females were present until all wasps had ceased to provision for the day. On 5 days in 1982 that were too windy or too cool for wasps to provision, some were active.

Most female *S. trilineata* activity was observed where wasps were provisioning. Individuals often stayed in an

area of a few square meters for several days if wasps were provisioning nearby. Some marked individuals were found outside the study site in other wasp nesting areas, up to 60m away.

In the sand scrape, female *S. trilineata* sat on small stones, short sprigs of vegetation or exposed lumps of sand. They turned and oriented toward most objects that moved in their field of vision. Individuals did not appear to attend more to any particular type of movement. All marked individuals darted at most moving objects passing through their field of view (Fig. 2). When 5 stones were tossed in front of a female *Senotainia*, at least one stone and often 4 or 5 were approached. Individuals varied in how often they approached a given species of wasp, but all individuals flew toward over 25%, usually more than 35%, of the individuals of each wasp species that passed through a 0.5m² field of view in front of them (Fig. 2). Many individuals darted at or followed for a short distance grasshoppers, butterflies, tiger beetles and miltogrammine, muscoid, asilid and bombyliid flies. During two days of observation, one individual flew at or followed a wind-blown *Lygodesmia* seed, asilids, muscoids, eumenids, chrysidids, mutillids, members of five families of bees and three species of sphecids. Another individual flew at or followed miltogrammines, bombyliids, muscoids, mutillids, eumenids, chrysidids, members of two families of bees and ten species of sphecids. All individuals flew toward a wide variety of aculeate

hymenopterans.

As *S. trilineata* females approached a moving object, they appeared to be able to discriminate more detail since they usually did not continue to follow unless it was a bee or wasp (Fig. 3). Wasps with prey, such as female *P. gibbosus* or *C.argusinus*, were often followed for longer distances. If the wasp or bee they were following landed, the fly usually sat within 10cm and waited, or infrequently, approached and attempted to make contact by jumping at the sitting bee or wasp. When a prey-laden wasp landed at her nest entrance, the following *S. trilineata* quickly approached the wasp as she entered the nest, whether she had to remove a temporary closure or not. Sometimes the fly entered the burrow with the wasp, emerging 1-5 seconds later. Frequently the *S. trilineata* landed on the prey then touched the prey with her abdomen. This occurred either while the wasp was removing the closure or just as she entered the burrow. Landing, contact and deposition of larva happened almost instantaneously, often in less than 1 second. Other wasp-like insects, especially epeoline bees, also were jumped at or followed into holes in the same way sphecids were.

Attempts to contact were not frequent and were only directed at aculeate hymenopterans which were, or closely resembled, solitary wasps. Several marked females contacted or attempted to contact a variety of wasps (with and without prey) and bees (Table 3).

All six wasp species were followed during provisioning flights by female *S. trilineata* and the flies also followed many other species of provisioning wasps that were nesting in the sand scrape. The frequency of following varied greatly among the six wasp species and in some species the frequency changed between years (Fig. 4). Also, the frequency with which *S. trilineata* contacted the prey during followed flights differed among the six species (Fig. 5).

Provisioning Flights and Way of Life of the Wasps

Females of all six species of digger wasps prepared nests of 1 to several cells, 10-40cm deep, in the sandy soil of the sand scrape prior to provisioning. Table 4 compares some aspects of the natural history of the six species of wasps. Prey were captured outside the sand scrape and carried back in flight, to the vicinity of the nest, tucked under the wasp's thorax and/or abdomen. Flights from the site of capture to the nest vicinity were not studied.

Oxybelus uniglumis

These wasps were active from mid-June until mid-September. At least two and probably three generations were represented. As many as 20 provisioning females were present each day during early July both years, and in late August in 1982 (Fig. 6). The nests were located throughout the flat and sloping parts of the sand scrape. Provisioning occurred throughout the day, on many days earlier and later

than any other wasps provisioned. During a provisioning bout females retúrned every 1-4 minutes with prey. Many females provisioned two cells in a nest in one day and started a new nest every second or third day. A variety of dipterans were taken as prey, with anthomyiids being the most prevalent. Also taken were dolichopodids, syrphids, sarcophagids and muscids. One male *S. trilineata* was taken from a provisioning female. Prey items dropped by female *B. americana* and *C. argusinus* were occasionally retrieved by female *O. uniglumis*, but otherwise different species of flies were used as prey by these three fly-hunters. Seven to eleven prey were placed in each cell, with the number depending on the size of prey used. All aspects of the nesting behaviour of this species concur with the summary of *O. uniglumis* behaviour by Peckham *et al.* (1973), except that the density of nests was much higher than they report.

These wasps usually approached the nest with a quick flight 0.5-1.5m above the ground, carrying the prey with their middle legs. They appeared to fall out of the sky, within 2m of the nest. After they tumbled to the ground, they impaled the prey on their sting, sat for 1-5sec, then proceeded fairly directly to the nest by a series of short (0.03-1m), low (<0.05m) flights interspersed with bouts of walking (Fig. 7). Females moved quickly while provisioning. At the entrance the female removed the temporary closure in a few seconds (X=9.1±8.5sec, N=91) and walked into the entrance, with the prey still impaled on her sting (Plate

5). A few females took a less direct route to the nest or sat for over 10 seconds before entering. Peckham *et al.* (1973) have described a similar flight for this species.

Twenty of 692 provisioning flights were followed, in approximately equal proportions in 1981 and 1982 (9/219 vs 11/473, $p>0.10$, Fig. 4). Contact at the nest entrance occurred during 5 of the 20 followed flights (Fig. 5). Four types of followed flights were discerned. In six instances the *O. uniglumis* turned and flew at the *S. trilineata*; one prey was contacted. Twice, followed females approached the nest by an indirect flight path; one of these was contacted. Once the female dropped her prey and left the area. The other eleven followed flights were direct to the nest, similar to most non-followed flights; three resulted in contact. Dropping prey and charging other insects were also responses to disturbances other than *S. trilineata*. Peckham *et al.* (1973) noted followed flights where females dropped their prey. Females removed the temporary closure as quickly during followed ($\bar{X}=5.4\pm3.9$sec, $N=9$) as non-followed flights (see above). In 1981, 4/9 and in 1982, 1/11 followed flights were contacted. Three of the contacts occurred when the fly followed the wasp into the nest entrance; the other two when the fly landed and touched its abdomen to the prey at the entrance.

Contacted flights were infrequent, 4/219 flights in 1981 and 1/473 in 1982. Since about 9 prey were placed in

each cell, one of every 15 cells was provisioned with a contacted prey. Maggots were found in 4 of 29 cells from 7 nests examined, three of these were in one nest. Because of the large size of the maggots and pupae in these four cells, and the prevalence of *Phrosinella fulvicornis* larvipositing at the entrances to *O. uniglumis* nests, they were presumed to be maggots *P. fulvicornis*.

Crabro argusinus

These wasps were active from late June until late August 1981 and until mid-September 1982. Peak activity of 10-15 provisioning females per day was observed in early July in both years and in August 1982 (Fig. 6). In 1981 there was a small second generation in mid-August, in 1982 a large second generation in late August. Nests were found on the flat and sloping areas of the sand scrape. Several nests were frequently clumped in a few square meters rather than being evenly spaced throughout the area. The position of these patches changed between and within nesting seasons.

The prey were all dipterans belonging to two families. More than 90% of the prey were dolichopodids; ephydrids were also taken, especially in September 1982. Two provisioning bouts were often noticed on most days, one around noon and a more sustained one between 1700 and 1900. During these bouts females returned every 2-3 minutes with prey. From 7-17 prey (X=11.3, N=15) were provisioned in each cell of the multicellular nests. Nest placement, prey and

provisioning periods are all consistent with previous reports for this species (Evans 1960; Matthews *et al.* 1979; Evans *et al.* 1980). Many females abandoned their nests every 2-4 days. They either started a new nest or usurped the nest of another female, in a manner similar to that described for *C. monticola* (Alcock 1982).

Females returning with prey flew very quickly to within 0.5m of the nest, at an elevation of less than 0.25m. They then flew backwards, facing the nest, 0.01-0.1m above the ground, while moving their body side-to-side. The result was a slow, pulsating flight away from the nest, which I called a zigzag. Usually 1 to 3 zigzags, 0.05 to 0.40m in length, were performed before the wasp flew very quickly to the nest and plunged through the open or partially closed entrance (Fig. 7). Throughout the flight the prey was held with one or both of the middle legs of the wasp. As the wasp plunged through the entrance, the prey was shifted from under the thorax to under the abdomen and part of the prey was exposed beyond the tip of the wasp's abdomen (Plate 6). A few of the initial or final approaches were slower because the wasp sat near the nest before entering (16/1078). Infrequently females performed some flights which lacked zigzags (37/1078). Several females, especially the few which provisioned in June 1982, rarely zigzagged. During the provisioning of a nest by one female, the position of the zigzags relative to the nest entrance and the direction of the fast approach did not vary appreciably. The

characteristic waver of provisioning females approaching the nest has been noted in all studies of this species (Evans 1960; Evans *et al.* 1980; Matthews *et al.* 1979). Matthews *et al.* (1979) also recorded a nesting aggregation where females did not perform zigzags.

Of 1200 flights, 14% were followed during both years (59/413 and 109/787, $p>0.10$, Fig. 4). The frequency of following did not change significantly throughout the day (Fig. 8). *S. trilineata* females made contact during 8 out of 158 followed flights with known outcomes (Fig 5).

Contact during followed flights was equally probable in 1981 and 1982 (2/52 vs 6/106, $p>0.10$). Zigzags were longer and more numerous during followed than non-followed flights (Fig. 9). Three types of followed flights were observed, in a sample of 122. During 11 followed flights (9%), the female wasp dropped her prey and left the nesting area. Only one of these appeared to drop the prey in response to a female *S. trilineata* contacting it. In another 12 (10%), the female performed either only short zigzags (<0.5m) or none at all, and of these 12, five were contacted. Most commonly, in 99 instances (81%), zigzags were much longer, both in length and duration when a *S. trilineata* was following (Fig. 7). When the wasp flew in and started to back up, the *Senotainia* started to follow. The wasp and fly were face to face as the wasp flew backwards, with the fly following most pulses of the zigzag. This usually continued for over 1m, sometimes for over 3m and rarely up to 6m,

until the following *S. trilineata* sat down. After the fly sat, the wasp slowed her backwards movement while still wavering back and forth 5-30cm in front of the fly. After a few seconds of this hovering the wasp flew quickly back to the vicinity of the nest, zigzagged once or twice and entered quickly if the fly had not followed her back to the nest. If the wasp was followed the process was repeated. Almost invariably these long zigzags lured the *S. trilineata* away from the nest entrance and left the fly sitting 1-3m away while the female *C. argusinus* entered unmolested. Only three of the 99 flights with long zigzags were contacted. The followed zigzags were much longer than zigzags during non-followed flights ($\bar{X}$=1.6m vs $\bar{X}$=0.25m, N=166 and 260, $p<0.01$,). Likewise individual zigzags during followed flights, that were not followed by a *Senotainia*, were much shorter than zigzags that were followed during the same flights ($\bar{X}$=0.3m vs $\bar{X}$=1.6m, N=203 and 166, $p<0.01$, Fig. 10). Zigzags over 1m in length were performed only when a female *S. trilineata* was following. The attraction of the zigzags to satellite flies has been reported by Evans (1960) and Matthews *et al.* (1979).

Rarely short zigzags (less than 0.5m in length) were performed in apparent response to nearby flies that did not follow the zigzag. In these situations the zigzags were more time consuming than the short zigzags of non-followed flights, lasting from 10-30 seconds compared to 1-5 seconds. Most of these zigzags, like the long zigzags, were seen in

response to *S. trilineata* females, but on four occasions they were observed in response to another kind of fly. Three of these were in response to adults of the miltogrammine, *Phrosinella fulvicornis*, circling within 10cm of the nest entrance. The wasp performed 1-5 time consuming zigzags directly in front of the fly until it moved more than 50cm from the nest. Only once did the *P. fulvicornis* follow a zigzag and then for only a few centimetres. Once, time consuming zigzags were performed in front of a male sarcophagid fly which had followed a previous zigzag for about 20cm. Live flies (sarcophagids or calliphorids) pinned 2-5cm from the nest entrance did not elicit this behaviour (N=12).

Time consuming zigzags were recorded during two followed flights that resulted in contact. On both occasions the *S. trilineata* sat near the nest while the *C. argusinus* slowly hovered and zigzaged backwards 5-30cm in front of the fly. The wasp repeated this as many as 9 times. The satellite fly ignored each of these zigzags or less frequently, followed for less than 15cm. Eventually the wasp entered her nest and the *S. trilineata* followed her into the entrance.

Contact was infrequent and in about equal proportions in both years (2/406 vs 6/784, $p>0.10$). The satellite fly followed the wasp into the nest entrance during 6 of the 8 contacts. In the other 2 the prey was touched by the satellite fly as the wasp approached the nest. Since about

11 prey were placed in each cell, 1 in 13 cells was provisioned with a contacted prey.

The only prey that I observed being contacted by a female *S. trilineata* harboured a maggot. This dolichopodid was contacted during a zigzag and was subsequently dropped by the wasp and was immediately collected. Initially no maggots were seen, but two days later the dolichopodid was consumed except for the exoskeleton, and two miltogrammine maggots were in the body cavity. Other prey were examined 1-10 days after being collected during followed flights with no contact (N=5) and non-followed (N=10) flights. No other maggots were found. Twenty four cells from seven nests were dug. Four maggots were recovered. One *Metopia argyrocephala* was successfully reared in the laboratory. The other three maggots were probably those of *S. trilineata*; two of these were in one nest.

Bembix americana

Female *B. americana* provisioned from mid-July until mid-September. Very few (less than 5 provisioning females/day) were present until late August, after which time as many as 30 provisioning females were present each day (Fig. 6). Presumably these wasps represent one generation with variable emergence times, but it is possible that a small first generation is represented. Nests were on the flat or sloped areas of the sand scrape. In 1982, the number of nests dwindled as many nested in sandy areas

around the scrape, including sand flats along the river exposed by lower water levels, instead of in the sand scrape.

While the female was not at the nest entrance, a temporary closure was maintained. A variety of dipterans were taken as prey, including asilids, bombyliids, syrphids, sarcophagids, anthomyiids and muscids. The sizes of the prey used varied as much as their taxonomic affinities. Twenty to thirty prey were placed in each nest during a period of five to ten days. Only 1 or 2 prey were brought in on each of the first 3-5 days. As many as 10 prey were provisioned on each of the last 2 days that the female provisioned the nest. During provisioning bouts on the last two days of provisioning, females returned every 2-10 minutes with prey. More than 90% of the provisioning took place between 1000 and 1800, with no obvious peak within this time. Nest characteristics, types of prey and the progressive provisioning of cells during a period of several days are consitent with previous studies (Evans 1957, 1966a).

Provisioning flights were very fast and direct to the entrance at an elevation of 0.05-0.5m (Fig. 7). In the last 0.3m, the flight slowed as the wasp banked down to the entrance. The temporary closure was quickly removed ($\bar{X}$=6.05 sec, N=65) and the wasp entered, shifting the prey from the middle to hind legs (Plate 7). Rarely, the flight took longer because the female sat near the nest.

Thirty-nine of 540 flights were followed, about equally in 1981 and 1982 (30/350 vs 9/190, $p>0.10$, Fig. 4). Following frequency did not change significantly throughout the day, although a decreasing trend was noticed (Fig. 8). Contact of the prey during a followed flight was equally probable in 1981 and 1982 (26/30 vs 7/8, $p>0.10$, Fig. 5). Four types of followed flights were discerned; during all of these prey were frequently contacted. Quick and direct flights, the same as most non-followed flights, occurred on 24 followed flights; all of these were contacted. Contact occurred either as the female *S. trilineata* landed on the prey at the nest entrance or as it entered the nest with the wasp. On seven occasions the female wasp sat or flew off, returning 1-4 minutes later; 4 of these were contacted. Four times another female *B. americana* delayed flights by chasing the provisioning female; contact was seen 3 times. In two cases the provisioning *B. americana* chased the *S. trilineata*, yet on one of these occasions contact was observed. During flights that were not followed, provisioning females also left the area, were delayed by other females and chased other insects. The time taken to dig and enter was not different between flights where contact was observed and non-followed flights ($\bar{X}=6.43$sec vs. $\bar{X}=6.05$sec, $N=21,65$, $p>0.10$). At one nest the female did not place a closure at the entrance while away hunting. An *S. trilineata* followed her to the entrance and was able to touch the prey with her abdomen as the wasp paused briefly

at the entrance.

The proportion of total flights contacted was also about equal between years (26/350 vs 7/189, $p>0.05$). Since each cell was provisioned with 20-25 prey, all cells contained at least one contacted prey. However, the excavation of 12 nests produced only one fly maggot. Contact by a female *S. trilineata* was observed at five of these nests two to seven days before excavation, yet only one fly maggot was recovered. In this cell the wasp larva pupated the next day, very few of the provisions remained and the maggot died the next day. In the five remaining nests, where no *S. trilineata* larvipositions were suspected, no maggots were found.

Philanthus gibbosus

Females provisioned from mid-July until mid-September, with peak numbers (15-20 provisioning females per day) in early and mid-August (Fig. 11). All nests were on the vertical panel or on the near vertical parts of the slope; consequently no nests were excavated. Usually a temporary closure was in place while the wasp was away from the nest. All prey were aculeate hymenopterans, primarily small, dark halictid bees, but a few wasps were also taken (e.g. *Crabro* sp., *Tiphia* sp.). Provisioning was rarely seen in the morning, but in the afternoon there was often a peak from 1700 to 1900. Few females provisioned more than 4 or 5 times in one hour. In several nests more than one female

provisioned during one day, and through the season most nests were provisioned by several females. Prey, nest site and nest use are consistent with the reports of Evans (1973) and Evans and Lin (1959).

Females returning with prey approached the nesting area 2-3m above the nests. Once near the vertical panel they began a slow step-wise descent to within 1m of the entrance. Here they started a very conspicuous and vigorous waggling of their abdomen, the body held at a 45° angle to the vertical, with the head elevated, as they slowly descended directly to the nest (Fig. 12). Throughout, the prey was clasped with the middle legs (Plate 8). After removing the closure ($\bar{X}$=4.8±3.9sec, N=87), females shifted the prey from their middle to their hind legs and walked into the nest. Occasionally the waggle down to the nest was indirect or the wasp sat in the vicinity of the nest before entering. The slow descent to the nest by females of this species has been described both with (Reinhard 1924) and without (Cazier and Mortenson 1965) the conspicuous abdominal waggle.

Of 672 flights observed, 107 were followed, with significantly more being followed in 1982 than 1981 (9/127 vs 98/545, $p<0.01$, Fig. 4). Following frequencies did not change significantly throughout the day (Fig. 8). Contact was observed during most flights that were followed (73/102, Fig. 5). Contact occurred on the same proportion of followed flights in 1981 and 1982 (8/9 vs 65/93, $p>0.10$). Followed flights were very similar to non-followed flights,

including the conspicuous waggle (Fig. 12). The time taken to remove the temporary closure was not significantly different during non-followed flights (X=4.8±3.9sec, N=87), followed flights without contact (X=4.9±2.4sec, N=19) and followed flights with contact (X=4.2±2.5sec, N=48; All pairwise Mann-Whitney U-tests $p>0.10$). Three types of followed flights were discerned. Wasps approached the nest either directly or indirectly during followed flights. Contact was equally probable during both types of flights (36/45 vs 25/32, $p>0.10$). In a third type of flight (N=8), the female wasp turned and chased the following *S. trilineata*. Four of these were contacted. During all followed flights with contact, contact took place either while the wasp sat near the nest (9/54) or at the nest entrance (45/54). When contact took place at the nest entrance, the *S. trilineata* either landed and larviposited on the prey as the wasp removed the closure (38/45) or entered the nest with the wasp (7/45).

The prey of eight females was collected immediately after contact was seen. On four of these, maggots were visible when they were collected (Plate 9) or were obvious a few days later. No maggots were found on 2 non-contacted prey taken from females during followed flights and 8 prey during non-followed flights. In total, 73/672 flights were contacted. Assuming a conservative 10 prey per cell (Krombein *et al.* 1979), and that half the contacts represented larvipositions, about half the cells provisioned

included a contacted prey.

Philanthus inversus

This species was never very abundant, with a maximum of 10 provisioning females active on any day between mid-August and mid-September during both years (Fig. 11). Nests were situated on partially eroded surfaces of the vertical panel, within 1m of many *P. gibbosus* nests. The entrance was left open. Over 95% of the prey taken were male halictid bees of the genus *Agapostemon* and all other prey were halictid bees. In Colorado, male *Agapostemon* also constituted over 90% of the prey taken by this species (O'Neill and Evans 1982). Females rarely provisioned in the morning. In 1982 they provisioned throughout the afternoon, while in 1981 there was a definite peak from 1700 to 1900. Individuals were seldom seen to provision more than 2 or 3 times in one day.

Provisioning flights were characterized by their slowness and the wasp sitting near the nest. Most flights were fairly direct to the nest, with the wasp sitting, 1-8 times for 1-45sec ($\bar{X}$=11.1, N=89) on the ground, a root or a flower, within 2m of the nest, on 56/65 flights (Fig. 12). Females held the bee venter up, under their thorax with their middle legs. Some wasps paused very briefly at the open nest entrance.

Twenty eight of 109 flights were followed, with significantly more being followed in 1982 than 1981 (4/43 vs 24/66, $p<0.01$, Fig. 4). Followed flights, whether contact

occurred or not, did not differ from non-followed flights in general pattern or the number or duration of sits (Table 5). Both followed and non-followed flights were either direct or indirect. Contact occurred during 6 of 25 followed flights (Fig. 5), either at the nest entrance or away from the nest while the wasp was sitting. In the remaining three instances the wasp left the nesting area while being followed and did not return to the nest in the next five minutes. An *S. trilineata* often sat and waited within 5-20cm of the wasp that it had been following, then followed the wasp for only a few centimeters or not at all as the female continued toward her nest (Plate 10). On only one occasion did the female *S. trilineata* fly at another wasp while sitting near a wasp it had previously been following.

In total, 6 of 108 flights were contacted. Assuming 8 prey per cell (Krombein *et al.* 1979), every third cell was provisioned with a contacted prey. One prey from a non-followed flight and one from a followed but not contacted flight were examined for maggots, but none were found.

Cerceris echo

C. echo females provisioned from mid-July until late August 1981 and until early September 1982. Numbers increased through July to a peak of 80-100 provisioning females per day in early August and then numbers gradually declined (Fig. 11). This was the most numerous wasp in the

scrape for most of both summers. Nests were located in hard-packed sand in the flat and sloping areas of the scrape. Females provisioned throughout the warm parts of the day. When an individual was provisioning a cell it returned every 2-3 minutes with a beetle. Beetles of the family Phalacridae were the exclusive prey, with 30-45 ($\bar{X}$=37.5, N=6) being placed in each cell, usually in one day. The nest entrance was left open. Most details of nesting behaviour agree with those reported by Evans (1971) and Evans and Rubink (1978). Many females inspected the nests of other females and frequently they usurped the nest of a conspecific. This resulted in the usurped female usurping another nest or starting a new one.

Females returning to the nest with prey flew very slowly, carrying the beetle by its antennae in their mandibles and sometimes supporting the beetle's elytra with their front legs. Descent from 0.5-1m in elevation was gradual over the last 2m of the flight (Fig. 12). Some flights were direct, while many included much meandering and circling of the nest entrance. Rarely the wasp sat near the nest. The wasps landed inside the nest entrance so that the prey, still held under the thorax, was never exposed at the entrance.

Of 1125 flights, 47 were followed, with significantly more following in 1981 than 1982 (18/259 vs 29/866, $p<0.01$, Fig. 4). Followed flights did not differ from non-followed flights in pattern, speed or height. Contact was observed

on the same proportion of followed flights in 1981 and 1982 (7/14 vs 14/29, $p>0.10$, Fig. 5). Contact was equally probable whether the flight was direct or indirect (6/16 vs 12/22, $p>0.10$). All contacts were recorded when the satellite fly entered the nest with the provisioning female. Female *S. trilineata* were not observed contacting the beetle prey in flight or at the entrance. Frequently a fly would follow a slowly flying wasp for a short distance (less than 0.5m), then return to its perch. Contacts were infrequent and were in about equal proportions during both years (7/255 vs 14/866, $p>0.10$). Since about 37 prey were placed in each cell, 2 of every 3 cells contained a contacted prey. Six nests were dug in the sand scrape and at a sandy area 8km away. Thirty-three cells were found, but no sign of any maggots was noted.

Discussion

As a provisioning female digger wasp approaches her nest she is exposed to detection by watching female *S. trillineata*. Provisioning flights could act as a primary defence against this nest parasite and reduce the probability of detection by making the wasp's approach inconspicuous. Evidence from this study suggests that this does not happen since movement could not be avoided and satellite flies detected movement.

Once a provisioning female is followed by a satellite fly, the wasp's behaviour could deter the fly from following further and larvipositing on her prey, a secondary defence. In two species females exhibited behaviour that prolonged the approach to the nest and reduced the probability of larviposition.

Females of the other species displayed no response to a satellite fly that consistently deterred larviposition. Some of these species are known to have other effective defences while others have no known defences.

Flight Diversity among Species as a Primary Defence

Provisioning flights by female digger wasps were extremely diverse in this nesting aggregation, as diverse as those Evans (1970) and Alcock (1973) have described for other nesting aggregations. Each of the six species studied was easily distinguishable by flight characteristics when returning to the nest with prey. The speed, height above ground, directness, the angle at which the body was held and

body vibrations combined to make each species' flight distinct. Limited variation of these characteristics existed within each species, but it did not obscure the distinction between species. Based on the same characteristics, the flights of provisioning females were noticeably different from the flights of nonprovisioning females and males of the same species. The less common nesting species also had distinct flights, adding to the diversity present. For example, females of *Hoplisoides placidus* slowly descended to their nest entrances from 2 metres straight above their nests, female *Miscophus* sp. made short hops directly to their nests from several metres away, *Philanthus pulcher* females flew low and slowly, stopping periodically as they approached their nests and female *P. sanbornii* flew in at a moderate speed and gradually descended from a height of 1 metre as they flew the last 2m to their nests.

Females of some species had similar flights, flying directly to the nest at a low elevation. Two of these *Isodontia elegans* and *Ectemnius dilectus* were identifiable by their flight speed. Only females of two others, *Bembix americana* and *Bicyrtes ventralis*, were difficult to distinguish. All wasps considered so far were able to carry their relatively small prey beneath them while they flew. Further diversity in pattern of return is present if wasps which walk with prey are included. For example, females of *Ammophila procera* and *Podalonia* sp. which walked forward

with caterpillars and some species of Pompilidae which walked backwards with spiders were present.

Flight diversity does not appear to play a role in primary defence because female *S. trilineata* frequently and consistently oriented towards, darted at and followed flights of all of the diverse types. Observations of marked individuals showed that individual satellite flies were generalists in noticing and following flying insects. All individuals darted at and followed a wide range of insects that were not suitable hosts, such as cuckoo wasps (Chrysididae), bees, other miltogrammines, muscoid flies and pebbles (see Figs. 2 and 3). Individuals also did not selectively notice and follow some types of wasp flights and not others; they followed all types of flights that they were exposed to. Some discrimination may take place as the fly follows an insect, since digger wasps in general were followed for a longer distance and time than other types of insects. The flies appear to detect movement and then approach to inspect for suitability. No pattern of movement found in provisioning flights is beyond the range of movements detected and approached by female *S. trilineata*. Since all types of provisioning flights are noticed and approached, flights can not function as a defence which reduces the probability of detection, a primary defence.

Other Factors Influencing Frequency of Following

Even though flight diversity did not appear to be a primary defence, the frequency of following varied within and among species. Several factors, such as time of day, number of *S. trilineata* females present and number and kinds of wasps present when provisioning took place, were probably involved in producing these variations. Evans *et al.* (1980) presented preliminary evidence which suggest that *Crabro monticola* may avoid satellite flies by provisioning when the flies are not active. I found no evidence of any species consistently provisioning when *S. trilineata* were not active. On several very windy or cool days, during which wasps did not provision, flies were active. On most days female *S. trilineata* were active before or within thirty minutes of the first provisioning wasp and until provisioning had ceased (Table 2). Occasionally one or more wasps provisioned when no flies were around; these episodes were not predictable by time of day or weather conditions.

The number of female *S. trilineata* present while wasps are provisioning probably affects the frequency of following. I noticed that the number of flies fluctuated from day to day and from hour to hour, both of which may affect the frequency of following. I did not quantify these fluctuations and there are no published estimates of *S. trilineata* densities. My subjective impression was that wasps were followed more frequently when more flies were present. It is interesting to note that the percentage of

all flights observed that were followed was very similar in both years, 9.1 in 1981 and 9.6 in 1982

Another factor which probably affected frequency of following was the number and kinds of other wasps provisioning at the same time. In July 1982, when *C. argusinus* was the most common species, 28% of its flights were followed. In August 1982 several female *C. argusinus* were provisioning along with many females of at least seven other species. Only 7% of the *C. argusinus* flights were followed, while 19% of those of the most common species, *P. gibbosus*, were followed. In July of both years most of the satellite flies were concentrated around the *C. argusinus* nests while in August most were on the panel near the *P. gibbosus* nests. Several marked flies moved from the flat part of the scrape to the panel as activity on the panel increased. The flies concentrated where wasps were active and therefore proximity of other active wasp nests may have affected the probability of a wasp being followed.

Provisioning Flights as a Secondary Defence

The flights of female *C. argusinus* were a very effective defence and those of female *P. inversus* were a moderately effective defence against *S. trilineata*. Once a female *S. trilineata* is following a provisioning flight, the wasp's behaviour may function as a secondary defence against the nest parasite. Three types of possible defences seen in this study include luring the fly away from the nest

entrance (Alcock 1974, 1975; Matthews *et al.* 1979), indirect progression to the nest (stop-start) promoting the distraction of the fly (Evans 1970; Alcock 1974, 1975) and flying at or chasing the following *S. trilineata*. Females of four of the six species used at least one of these possible defences during some followed flights with variable effectiveness.

The long zigzags of *C. argusinus* flights were a most effective luring defence against *S. trilineata*. Matthews *et al.* (1979) and Evans (1960) recognized that the zigzags were longer when a satellite fly followed and that they played a role in luring the parasite away from the nest entrance. My observations confirm their interpretations, except that I consider that the start of the final fast bee-line towards the nest to be predictable, not unpredictable. After the wasp had lured the fly away from the nest entrance, the fly usually sat and watched the wasp. Then the wasp hovered 5-30cm from the sitting fly for a few seconds before flying quickly back to the vicinity of the nest. Thus, the start of the fast flight to the nest is a predictable response to the fly sitting down.

On a few occasions, the satellite fly sat near the nest of a *C. argusinus* but did not follow the zigzags. Under these circumstances the wasp performed several short zigzags in front of the satellite fly, presumably in unsuccessful attempts to get the fly to follow her. This behaviour was also seen in a few cases where another fly, such as the

miltogrammine *Phrosinella fulvicornis*, was near the entrance when the wasp returned with prey, but not in response to pinned flies.

Luring zigzags appear to be a geographically widespread, facultative response to following flies by female *C. argusinus*. At two of three nesting aggregations Matthews *et al.* (1979) studied in Georgia, satellite flies were present and female *C. argusinus* performed zigzags during provisioning flights. At the third satellite flies were absent and female *C. argusinus* did not perform zigzags. Some females that provisioned in June 1982 at my study site, when very few female *S. trilineata* were active, employed flights which lacked zigzags.

The proportion of the eight contacts that were actual larvipositions is not known for *C. argusinus*. Two of these occurred in flight, just before the wasp entered the nest. Female *S. trilineata* are known to successfully larviposit on the prey of other sphecids at this point (Ristich 1956; Peckham 1977). Most of the contacts occurred when a *S. trilineata* followed the female into her nest. Immediately after the *C. argusinus* plunged through her nest entrance the prey trailed behind the abdomen. It was usually visible for 1-2 seconds, long enough for larviposition to occur. In all the other species studied, except *Cerceris echo*, the prey is exposed in a similar manner as the wasp entered the nest. Thus many of the contacts recorded with the *S. trilineata* following the wasp

into the nest probably resulted in larviposition. For *C. argusinus* and the other five species studied, the ratio of contacts to larvipositions is not known but is assumed to be species specific.

For flights to function as a defence against nest parasites they must reduce the probability of contact. Even though contact may not equal larviposition, it is a necessary first step for parasitism to occur. Nest excavation revealed that 3 of 24 *C. argusinus* cells were probably parasitized by *S. trilineata*, very close to the prediction of 1 in 13 cells. If all followed flights had resulted in a larviposition, every cell provisioned would have been parasitized. Even if only half of the followed flights had resulted in a contact, 3 of every 4 cells provisioned would have contained a contacted prey. The long zigzags dramatically reduced the probability of larviposition and therefore the mortality of *C. argusinus* larvae due to nest parasitism.

Alcock (1975) considers the responses of females of 5 species of *Philanthus* to satellite flies to be luring flights. However, data that can be used to assess the effectiveness of luring as a defence is available only for

maggot and, assuming a conservative 6 prey per cell (Krombein *et al*. 1979), all cells may have been parasitized. The luring flight does not appear to reduce the probability of larviposition to a low level in this species under the conditions reported.

The luring flights of females of three other species appeared to be responses to many types of disturbances which only incidentally deterred a following *S. trilineata*. Female *P. gibbosus* were considered by Alcock (1975) to have a luring response to satellite flies. He based this on Cazier and Mortenson's (1965) report of a female flying away from her nest when being followed. In this study only a few *P. gibbosus* flew from very close to their nests to a spot 1-3m away when they were followed (included as indirect flights in analysis). Females of two other species, *B. americana* and *O. uniglumis*, also occasionally responded to being followed by flying away from their nests. Peckham *et al*. (1973) reported that female *O. uniglumis* sometimes flew away from their nests when followed and in some instances dropped the prey they were carrying. In all three of these species, a flight away from the nest was a common response to a variety of disturbances, such as the approach

modification of this type of general response and an increase in its specificity towards female *S. trilineata* may have been the origin of the luring flights of *C. argusinus* and some species of *Philanthus*.

The interruptions (sits) in the flights of some *Philanthus* females, similar to those of *P. inversus* females, are thought to distract following satellite flies. Both Evans (1970) and Alcock (1974) have watched a satellite fly sitting behind a motionless female *P. crabroniformis*, fly off after another wasp, allowing the first to proceed to its nest unattended. This was seen only once in this study. More frequently the fly appeared to lose interest in the provisioning female as the time taken to get to the nest increased. Often satellite flies would fly off while the wasp was sitting, or just as she started to fly, not to follow another wasp, but to sit on a nearby perch. The slow approach, including sits, promoted the following *S. trilineata* to lose interest during the provisioning flights of this species. Both followed and non-followed flights had a similar number of sits. This suggests that the stops are a defence that is always in place, possibly because of the slowness of the approach and the

cells if all followed flights had resulted in a contact. Therefore the stops are moderately effective. For other species which employ stop-start flights, little data have been presented to confirm their effectiveness. Only for *P. multimaculatus*, which uses both stop-start and luring flights, are quantitative data presented and as discussed earlier the flights of these females do not appear to reduce the probability of larviposition. The effectiveness of this defence may depend on the number of satellite flies and the number of wasps provisioning at the same time if the flies are to be distracted. The importance of stops during the approach on followed flights is equivocal, being a moderately effective defence in *P. inversus*, and apparently unimportant in *P. multimaculatus*.

A rare response to being followed by females of three species, *O. uniglumis*, *B. americana* and *P. gibbosus*, was to turn and chase the following *S. trilineata*. Two of these are fly hunters and are known to infrequently take miltogrammines as prey. This may have enhanced the probability of the satellite fly ceasing to follow the wasp. Females of all three of these species responded to other wasps and passing insects in the same manner during some [illegible]ghts. This response, as with flying away [illegible]ppears to be a response to many disturbances [illegible]ecific defence against satellite flies. The [illegible]tally cause the *S. trilineata* to stop [illegible]reby reduce the chances of larviposition.

Diversity of Provisioning Flights as a Secondary Defence

Three types of followed flights deterred *S. trilineata* from contacting the wasp's prey with variable effectiveness. The effectiveness of each of these responses appeared to depend more on the behaviour of female *S. trilineata* than the presence of other types of responses. For aspect diversity to function as a defence an enemy must 1) use different cues to recognize each prey type or 2) not be able to recognize the modified cues displayed by each type of prey. Female *S. trilineata* used two aspects of wasp provisioning flights which were common to all of the diverse flights. First the satellite fly noticed movement, whether it was a walking, flying, fast or slow insect. Wasps cannot completely conceal their movement from a nest parasite that notices virtually all insect movement. The source of movement was followed if it was a wasp or wasp-like insect. Next, satellite flies appeared to cue in on a potential host if in its behaviour it resembled a wasp descending to and entering a hole. Contacts were attempted when wasp-like epeoline bees and even unwasp-like halictid bees entered holes. *C. argusinus* were followed into their nests by satellite flies that just seconds earlier had ignored zigzags, normally a very powerful stimulus. In contrast to a wasp entering a nest, prey items or nest holes alone were of little interest to a fly and did not prompt larviposition. Individual female *S. trilineata* were able to and did contact wasps and other aculeates during many

diverse types of flights. The only way a wasp could conceal its entry to its nest, from such a generalist, would be not to enter. The variation possible is limited to the speed at which the wasp approaches and enters. Aspect diversity will not work as a defence against a generalist nest parasite which cues in on the two essential and constant aspects of its host's behaviour that cannot be easily disguised: movement and entering the nest.

Convergent Provisioning Flights as a Secondary Defence

Three types of flights were recognized among those flights that deterred contact by female *S. trilineata*, but two of these appear to converge on a similar pattern. The flight patterns of female *C. argusinus* and *P. inversus* appear to converge on the same tactic, prolonging the flight to the nest. The slow flights of *P. inversus* and the long zigzags of *C. argusinus* were followed for long periods of time compared to the flights of the other species. Female *S. trilineata* lost interest in these flights as time passed and the wasp did not enter a nest. These wasps delayed their approach and entrance to the nest, thus depriving the fly of an immediate stimulus to larviposit and effectively reducing its impact on the wasp.

Two other types of flights may deter larviposition by female *S. trilineata*, although they are not well documented. First, the wasp could outmanoeuvre the satellite fly either with speed or manoeuvrability. The fast bee-line to the

nest in *C. argusinus* and some *Philanthus* females (Alcock 1975) may function in this way. However, satellite flies appeared to be just as fast and manoeuvreable as the sphecids in flight and were capable of following the bee-line of *C. argusinus*. Secondly, an aggressive charge at the following fly might also deter larviposition. As noted, it is likely to be most effective for species which are capable of harming the fly. These two types of flights appear to be of questionable value and are little used.

The flight patterns that are most effective and prevalent in deterring larviposition by female *S. trilineata* appear to have converged on tactics that cause the fly to lose interest in the flight before the wasp arrives at the nest entrance. The importance of other types of flight responses which deterred larviposition is probably minimal due to their infrequent occurrence. Although this might be interpreted as convergence on prolonged flight patterns, as Alcock (1975) states, more comparative data from a wider variety of sphecids are needed to assess the amount of convergence. My data suggest that the effectiveness of the flights of *C. argusinus* and *P. inversus* does not depend on the presence of other types of flights in the nesting site. Therefore, these flights should be just as effective in single species nesting aggregations as they are in multispecies nesting aggregations.

Provisioning Flights not Involved in Defence

The provisioning flights of four species did not appear to be involved in defence against satellite flies. Females of these species all flew directly to their nests and showed no consistent response to being followed by a female *S. trilineata*. In 3 of these species, a high percentage of followed flights resulted in contact.

O. uniglumis females, the one exception, were rarely followed and relatively few followings resulted in contacts. The following *S. trilineata* often only darted at or followed the wasp briefly. On the surface, this species appears to be very susceptible to larviposition. Being carried on the sting the prey is very exposed, especially during the few seconds it takes to remove the temporary closure of the nest entrance. Despite this, only 6% of the cells provisioned probably contained a contacted prey and none of the 29 excavated cells were parasitized by *S. trilineata*. Other studies of this species confirm that miltogrammine parasitism is prevalent, yet *S. trilineata* is infrequently responsible (Evans 1970; Peckham *et al.* 1973). The reasons why parasitism was so infrequent in this study are not clear. Perhaps other wasp species diverted the attention of *S. trilineata* from *O. uniglumis* or the flies recognize this species as a potential predator and avoid them.

All cells provisioned by female *B. americana* probably contained contacted prey because many flights were followed and most followed flights resulted in contact. However, all

of the nests excavated contained a healthy wasp larva, and only one impoverished maggot was recovered. *S. trilineata* are often found in the nesting aggregations of this species, but are rarely reported as nest parasites (Allen 1926; Evans 1957, 1966a, 1970). The general lack of miltogrammine parasitism has been attributed to progressive provisioning (Evans 1966a). Prey are brought to the cell over a period of several days as the wasp larva develops. In most sphecids, prey are provisioned, the egg layed and the cell closed in 1 day or rarely 2. Therefore when a first instar miltogrammine larva is introduced into most sphecid nests, it is larger and more active than the wasp egg. The maggot can then outcompete the wasp larva for food or in many cells consume the wasp egg (Evans and Kurczewski 1966; Evans 1958). With progressive provisioning, only a few prey are provisioned when the wasp larva is smaller than the first instar miltogrammine maggot. Most prey are provisioned after the wasp larva is larger than the maggot, probably resulting in the wasp consuming or outcompeting the maggot. Some *S. trilineata* larvae may be successful if they are introduced very early in the nesting cycle. There may also be a very short period of time during which introduction may result in the survival of both the wasp and the fly (Evans 1966a). Healthy wasp and miltogrammine larvae have been found in the cells of two progressive provisioning wasps, *B. americana* and *Rubrica surinamensis* (Rau and Rau 1918; Evans 1957, 1966a; Evans, Matthews and Callan 1974) but such

occurrences have not been recorded in any sphecid which does not provision progressively. Progressive provisioning is probably a very effective post-larviposition defence against miltogrammines, but there is still no direct evidence on how the wasp larva and the maggot interact in the nest.

Behaviour of female *P. gibbosus* during provisioning flights was extremely conspicuous, especially the abdominal waggle. Widely separated populations employ this waggle (Reinhard 1924), while other populations do not (Cazier and Mortenson 1965). The function of the waggle is paradoxical because it appears to attract and keep the attention of female *S. trilineata*, a known nest parasite (Reinhard 1924; Cazier and Mortenson 1965; Barrows and Snyder 1973). Provisioning flights were frequently followed, but the flight pattern did not change in response to the satellite fly.

On most followed flights the prey was contacted and maggots were later found on half of the prey checked. One of every 2 cells provisioned probably contained a prey with a miltogrammine larva. Assuming half the contacts resulted in a parasitized cell, this would result in a higher frequency of nest parasitism than has been reported for any species in the genus *Philanthus* (Evans and Lin 1959; Evans 1970).

It is likely that a post-larviposition defence exists in species such as *P. gibbosus* where most followed flights result in contact. In this species grooming of prey by

females may be such a defence. I observed one female probing her contacted prey with her mouthparts while in a collecting net. Subsequently I failed to find a maggot on this bee. Similar probing or malaxating behaviour has been observed in several sphecids (e.g. *Chlorion aerarium*, *Prionyx parkeri*, *Liris nigra*, *Tachysphex terminatus*, Peckham and Kurczewski 1978; Steiner 1971, 1982; Spofford *et al*, 1982). In these species malaxation has many functions from drinking and feeding to preparation of egg-laying site and possible removal of other females eggs or miltogrammine larvae from the prey. Many female digger wasps, including *P. gibbosus* will usurp the nest (Evans 1973; pers. obs.) and presumably the nest contents of other females of the same species. When this occurs there would be an advantage to groom prey and thereby remove the egg of the previous nest occupant. If all prey were probed, probing took place soon after contact and much of the prey's body was probed, miltogrammine larvae would also be removed to the advantage of the grooming female.

The flights of *Cerceris echo* were followed infrequently and about half of the followed flights resulted in contact. Females did not respond to the following fly, but the fly often ceased to follow the slow flight before a wasp arrived at her nest entrance. Satellite flies may have paid little attention to this species because of the numerous nonprovisioning females and males present, which may have promoted habituation towards this species. Two out of every

3 cells provisioned contained a contacted prey, yet no maggots were found in the 33 excavated cells. In the only other studies of this species, no maggots were found in 7 cells (Evans 1971; Evans and Rubink 1978). Something is preventing *S. trilineata* from successfully parasitizing this species. The prey is very well protected under the thorax during the return flight and this may, as Evans (1963) has suggested, result in *S. trilineata* being unable to deposit larvae on the prey. All contacts observed for this species occurred when the fly entered the nest with the wasp, where contact with a well protected prey may be impossible. It is also possible that *Senotainia* maggots either can not enter the beetle prey to start to feed or that most beetles are unpalatable to these maggots. Taking beetles as prey may function as a defence against miltogrammines in these ways because miltogrammines, especially *S. trilineata*, are almost never reared from the nests of beetle hunting *Cerceris* (Evans 1971; Krombein *et al.* 1979).

Conclusion

Nest parasites, such as *S. trilineata*, are thought to be one of the most important factors shaping the behaviour of female digger wasps (Evans 1966a, 1970; Evans and Eberhard 1970). Most species of sphecids that have been intensively studied exhibit some type of defence against nest parasites (e.g. Tsuneki 1963; Evans 1966a, 1970; Peckham 1977). Many digger wasps have evolved some type of defence against *S. trilineata*, although the exact form varies greatly. Most types of flights are detected by *S. trilineata*, therefore effective defences must reduce the probability of larviposition or the impact of maggots in the nest. Provisioning flights by females of two of the species studied appear to have evolved characteristics that deterred satellite flies from larvipositing on their prey. In those species where females did not use provisioning flights as a defence, some other behavioural defence is either known (*B. americana*, progressive provisioning, Evans 1966a) or suspected (*P. gibbosus*, prey grooming, *Cerceris echo*, inaccessible prey carriage, pers. obs.).

The wasp populations that *S. trilineata* are exposed to have influenced the behaviour of this parasite. Female *S. trilineata* are generalists. They notice, follow, and most importantly, parasitize a wide range of sphecids. Host populations fluctuate within and between years due to changes in prey populations, parasite populations and the influence of weather. The sites of nesting aggregations

also change over the years. The spectrum of hosts available is constantly changing and this may have led to the lack of specialization in the searching behaviour of female *S. trilineata*. There has been little opportunity to evolve a counter defence against an effective defence of any one wasp species.

The interactions between host and parasite are necessarily constrained by many biotic and abiotic factors. Each species of wasp has evolved a slightly different defence because of its unique evolutionary constraints. Availability of prey and nest sites vary among species, as do the capabilities for flight and the impact of other nest parasites. These have all affected what type of defence against *S. trilineata* has been evolved in each species of digger wasp. The defences against a parasite exhibited by a group of digger wasps will be similar if their evolutionary constraints are similar. If their evolutionary constraints are dissimilar the defences will be dissimilar.

Table 1: The number of female wasps, nests and female *Senotainia trilineata* marked with individually identifiable marks.

	1981		1982	
	Wasps	Nests	Wasps	Nests
Oxybelus uniglumis	18	118	98	163
Crabro argusinus	24	93	70	120
Bembix americana	66	100	71	93
Philanthus gibbosus	22	65	53	56
Philanthus inversus	0	12	16	18
Cerceris echo	11	39	124	121
Senotainia trilineata	9		107	

Table 2: The time of first and last activity of female *Senotainia trilineata* compared to the first and last provisioning times by female digger wasps. All data are from 1982. Provisioning was infrequent in the first and last 30 minutes.

	Number of days
First fly present for more than 30 minutes before first provisioning	15
First fly present 1-30 minutes before first provisioning	8
First fly present 1-30 minutes after first provisioning	5
First fly present more than 30 minutes after first provisioning	0
Last fly present more than 30 minutes before last provisioning	3
Last fly present 1-30 minutes before last provisioning	9
Last fly present 1-30 minutes after last provisioning	6
Last fly present more than 30 minutes after last provisioning	6

Table 3: Aculeate Hymenoptera that marked female *Senotainia trilineata* contacted or attempted to contact. Letters refer to individual flies; some of which are also represented in Fig. 1.

S. trilineata	Aculeate Hymenoptera	
	Without prey	Carrying prey
E		*Bicyrtes ventralis*
F		*Bembix americana*, *Philanthus gibbosus*
L	Eumenid Wasp	*Lyroda* sp., *Philanthus inversus*
S	*Bicyrtes ventralis*, *Cerceris echo*	
T	*P. gibbosus*	*P. gibbosus*
U	*P. inversus*	*Ammophila* sp., *P. gibbosus*
V	*Sphecodes* sp.(Bee), *Ectemnius dilectus* *P. gibbosus*, Eumenid Wasp	*P. gibbosus*, *Cerceris echo*
W		*P. gibbosus*
X	Epeoline Bee, *Bembix americana*	*Bembix americana*
Y		*P. gibbosus*, *P. inversus*
Z	Eumenid Wasp	*Lyroda* sp, *P. inversus*
AA	Andrenid Bee	*P. gibbosus*
BB	Megachilid Bee Epeoline Bee	*P. gibbosus*, *P. inversus*
CC	Megachilid Bee *Bembix americana*	*Cerceris echo*

Species	Subfamily	Length (mm)	Prey	Prey Carriage	Prey /Cell	Cell Depth (cm)	Cells /Nest	Temporary Closure	Nest Switching
Oxybelus uniglumis	Crabroninae	7-8	wide variety of male Diptera 3-9mm	on sting	3-13	3-12	4-5	yes	no
Crabro argusinus	Crabroninae	9-11	primarily dolichopodid and ephydrid flies 3-12mm	middle legs	5-50	8-40	1-7	sometimes	yes
Bembix americana	Nyssoninae	15-20	wide variety of Diptera 3-20mm	middle legs	16-25	6-15	1 very rarely 2 or 3	yes	no
Philanthus gibbosus	Philanthinae	10-12	halictid bees, occasionally sphecids and colletid bees	middle legs	8-16	40-140	7-15+	yes	yes
Philanthus inversus	Philanthinae	12-14	halictid bees, >90% male *Agapostemon*	middle legs	?	?	?	no	rarely
Cerceris echo	Philanthinae	7-10	phalacrid beetles	mandibles with support from legs	30-45	8-60	>1	no	yes

Table 4: Summary of prey and nest characteristics of the six species of digger wasps studied.

Table 5: The duration and number of stops during provisioning flights by female *Philanthus inversus* that were not followed, followed with no contact or followed with contact

	Nonfollowed	Followed: no contact	Followed: contact
Mean Duration of Stops(sec)*	11.1±11.0 (N=89)	11.7±14.0 (N=36)	10.4±11.5 (N=12)
Number of Stops**			
0	9	2	0
1	32	4	3
2	14	2	1
3	5	2	2
4	2	1	0
≥5	3	3	1

* For all three Mann-Whitney pairwise tests $p>.10$.
** A Kolmogorov-Smirnoff two-sample test showed no significant difference in the distribution of the number of sits between nonfollowed and all followed flights, $p>.10$.

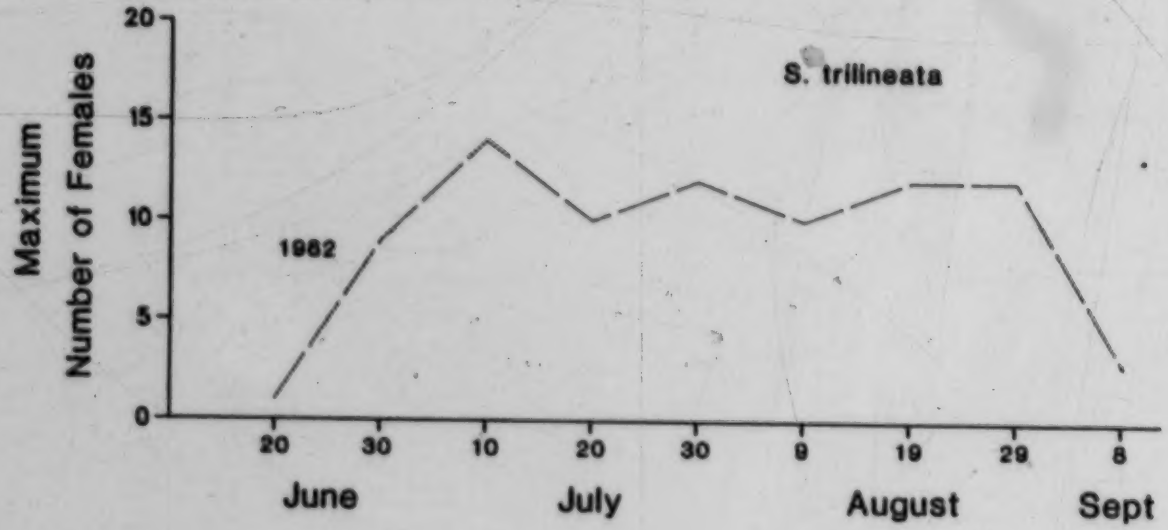

Figure 1: The maximum daily number of female *Senotainia trilineata* present during a ten day period beginning with the dates indicated on the X axis.

Figure 2: The reaction of individual marked female *Senotainia trilineata* to five types of aculeate hymenopterans flying through a .5m³ field of view in front of the *S. trilineata*.

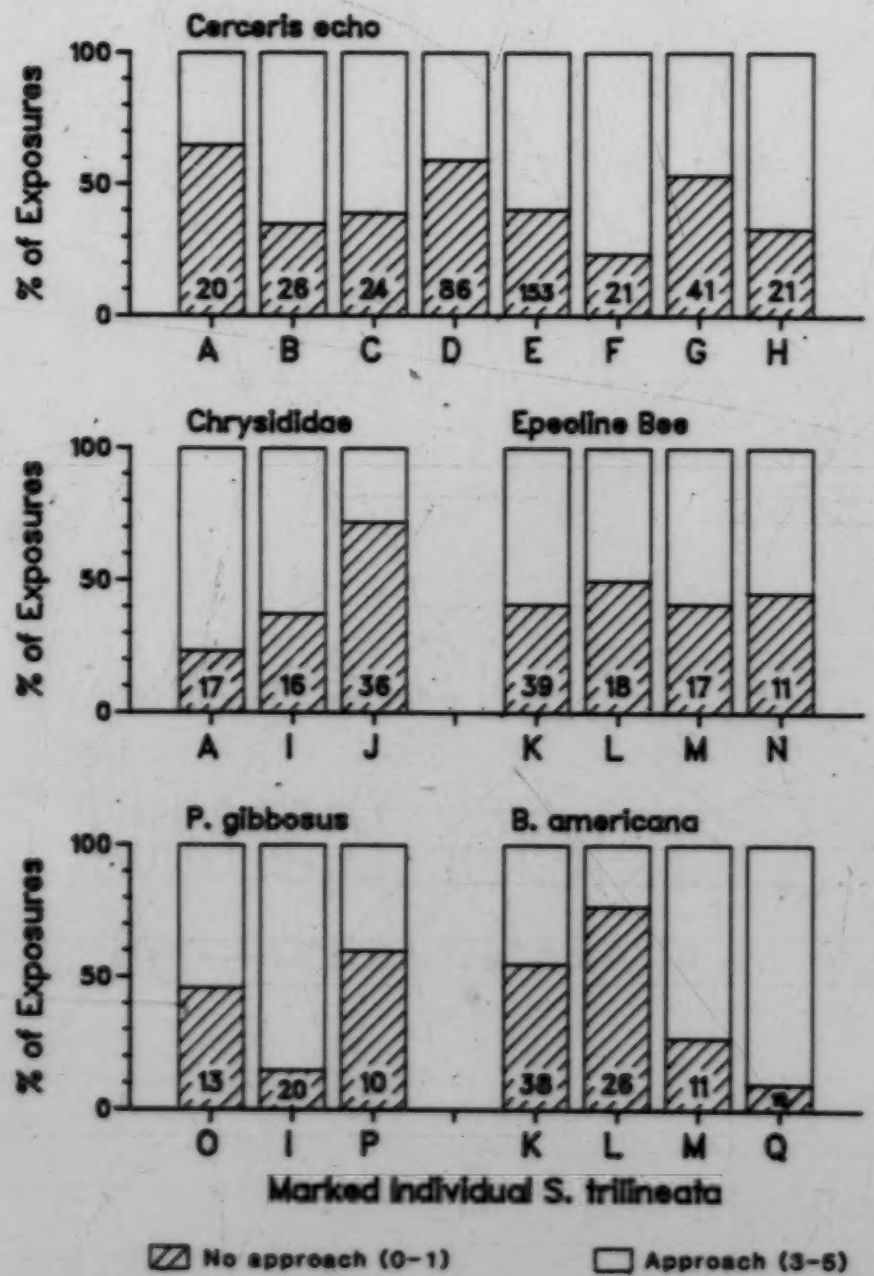

Figure 3: Summary of responses by all marked female *Senotainia trilineata* to pebbles, dipterans and aculeate hymenopterans passing through a 0.5m² field of view in front of each female. * denotes females carrying prey. Sample sizes are indicated.

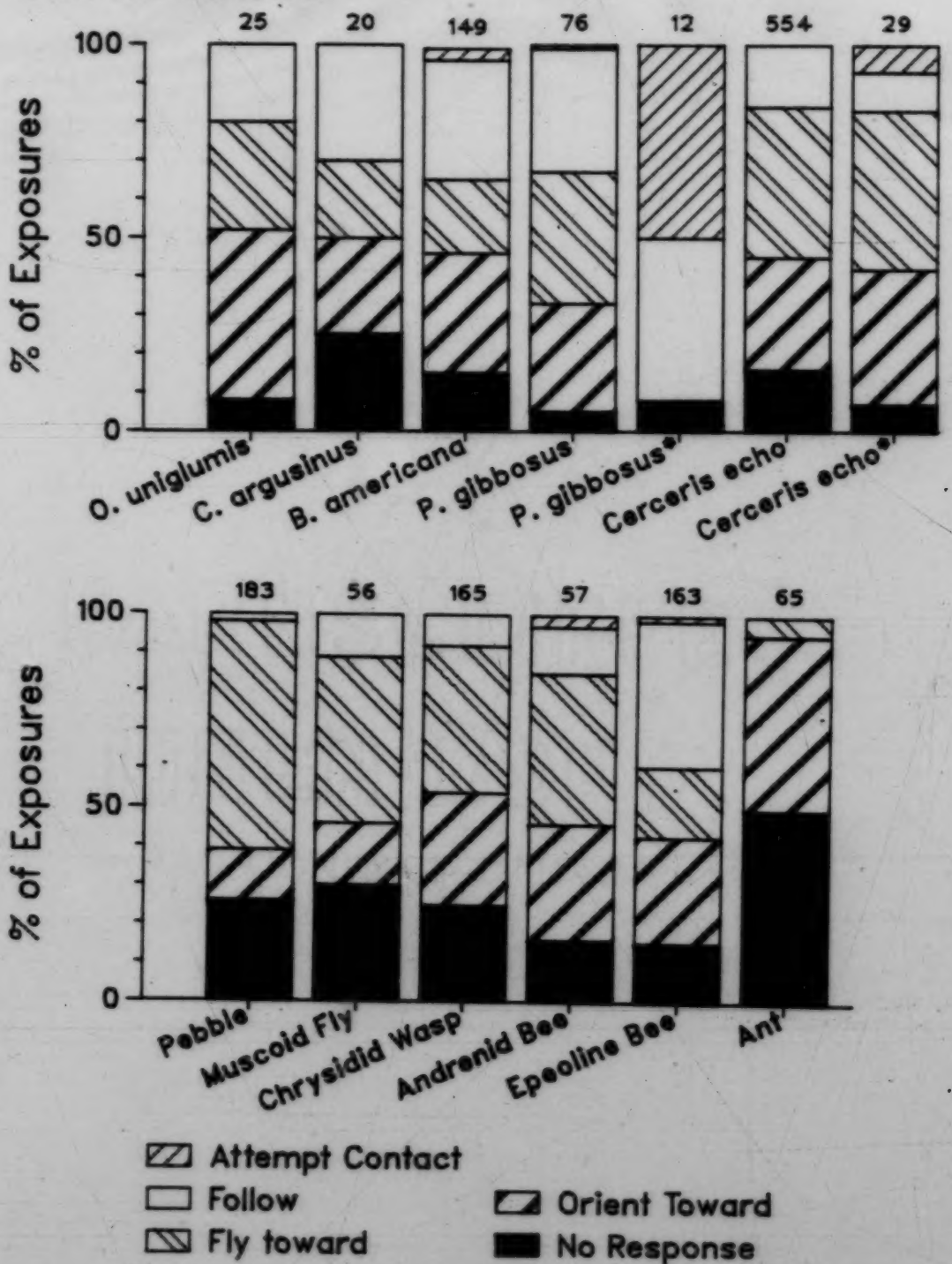

Figure 4: The percentage of provisioning flights that were followed by a female *Senotainia trilineata* in 1981 and 1982. * indicates a significant difference in the frequency of following between years at the 0.05 level.

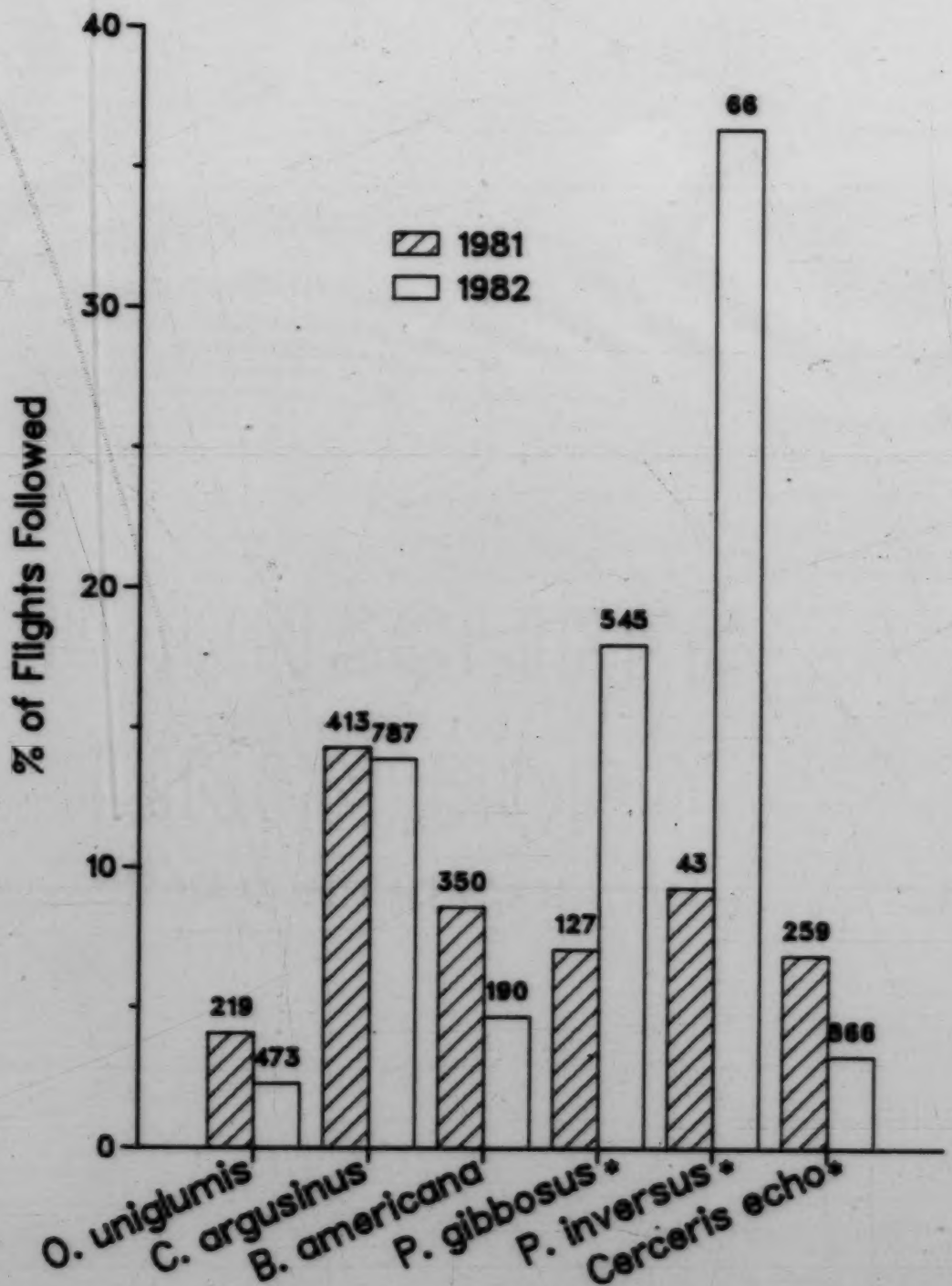

Figure 5: The percentage of followed provisioning flights that resulted in contact by a female *Senotainia trilineata*, 1981 and 1982 data combined.

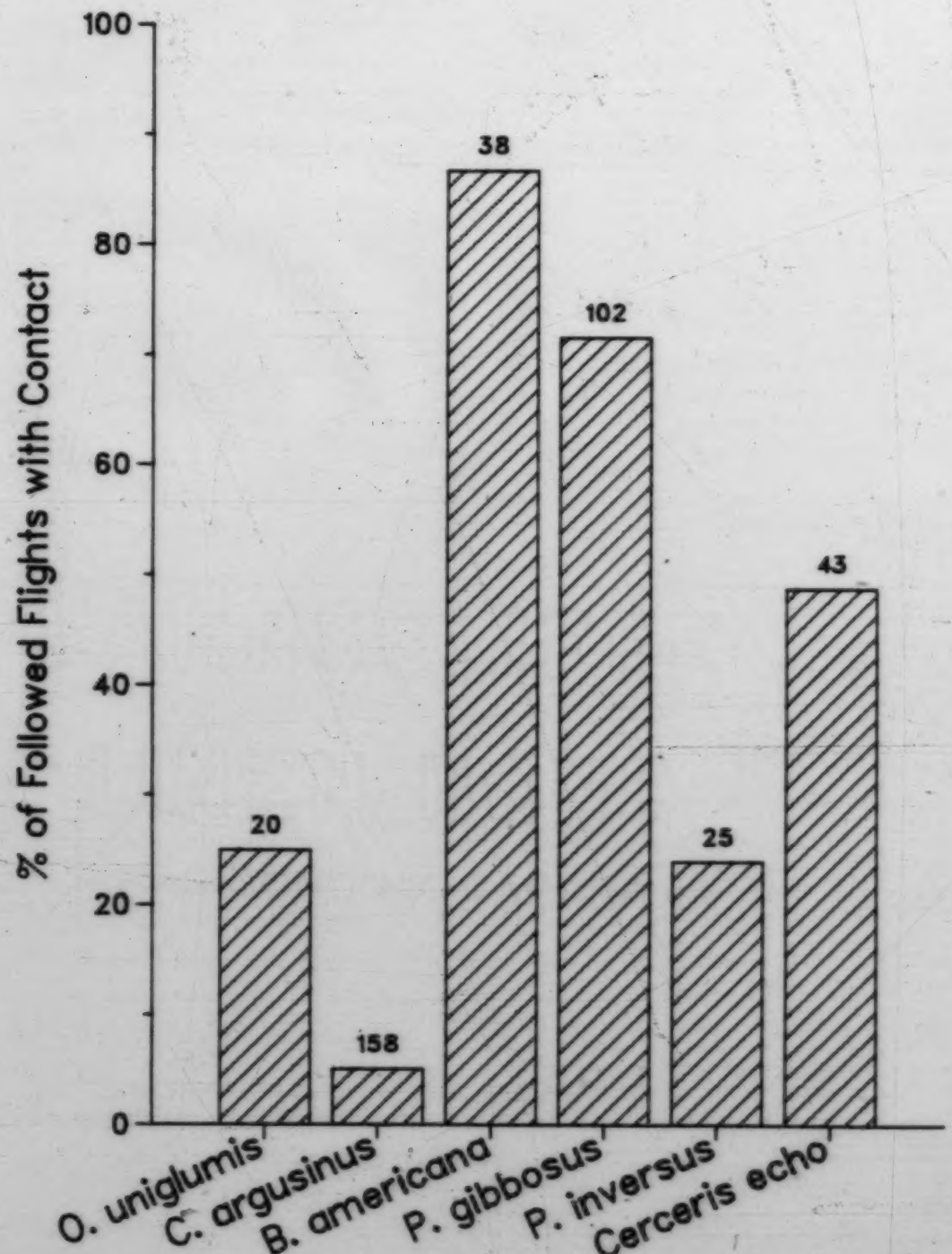

Figure 6: The maximum daily number of provisioning female *Oxybelus uniglumis*, *Crabro argusinus* and *Bembix americana* present during a ten day period beginning with the dates indicated on the X axis.

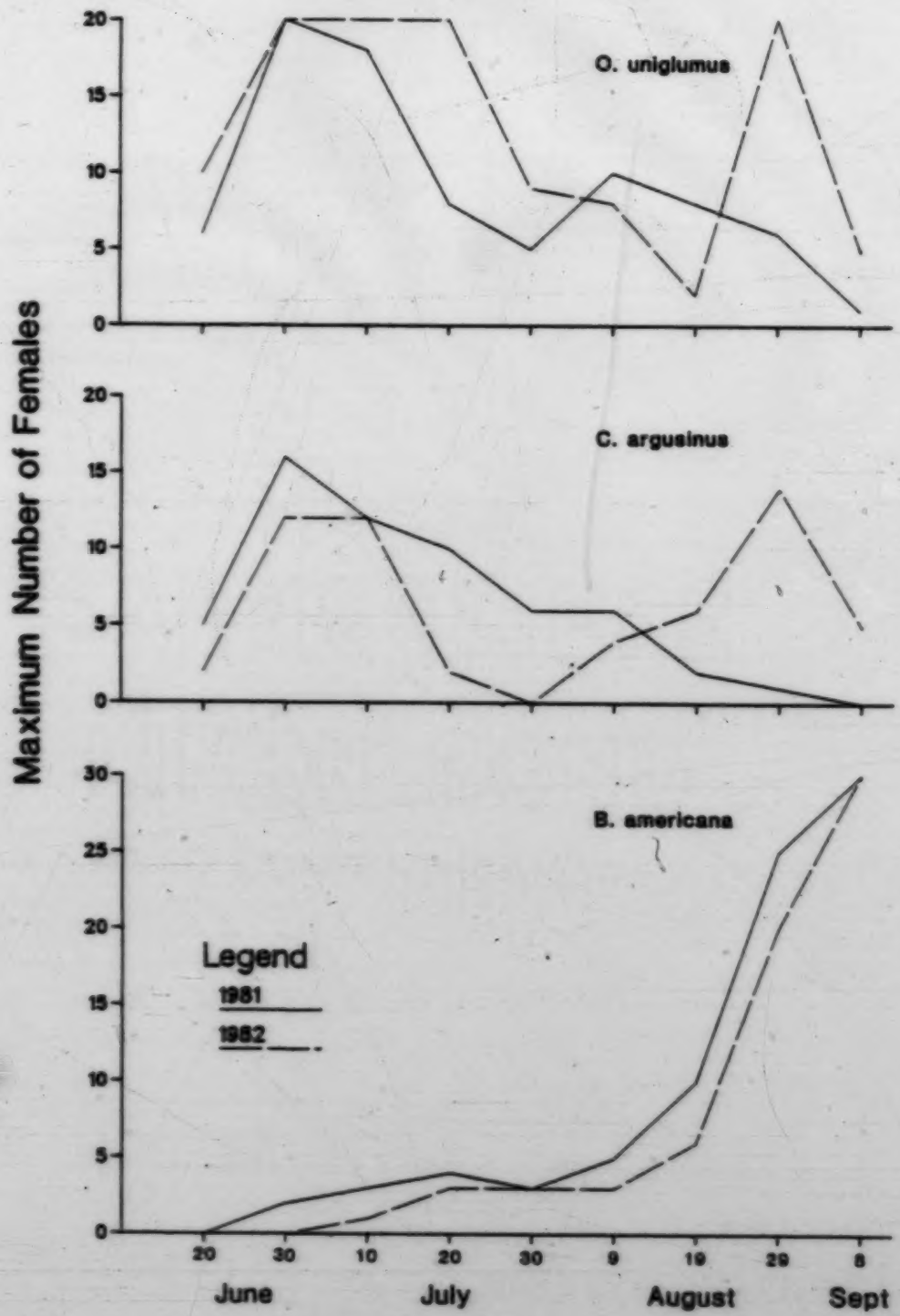

Figure 7: The typical pattern of provisioning flights of *Oxybelus uniglumis*, *Crabro argusinus* and *Bembix americana* females. All are top views.
o nest entrance. • wasp stationary.
~~~ backward zigzag.

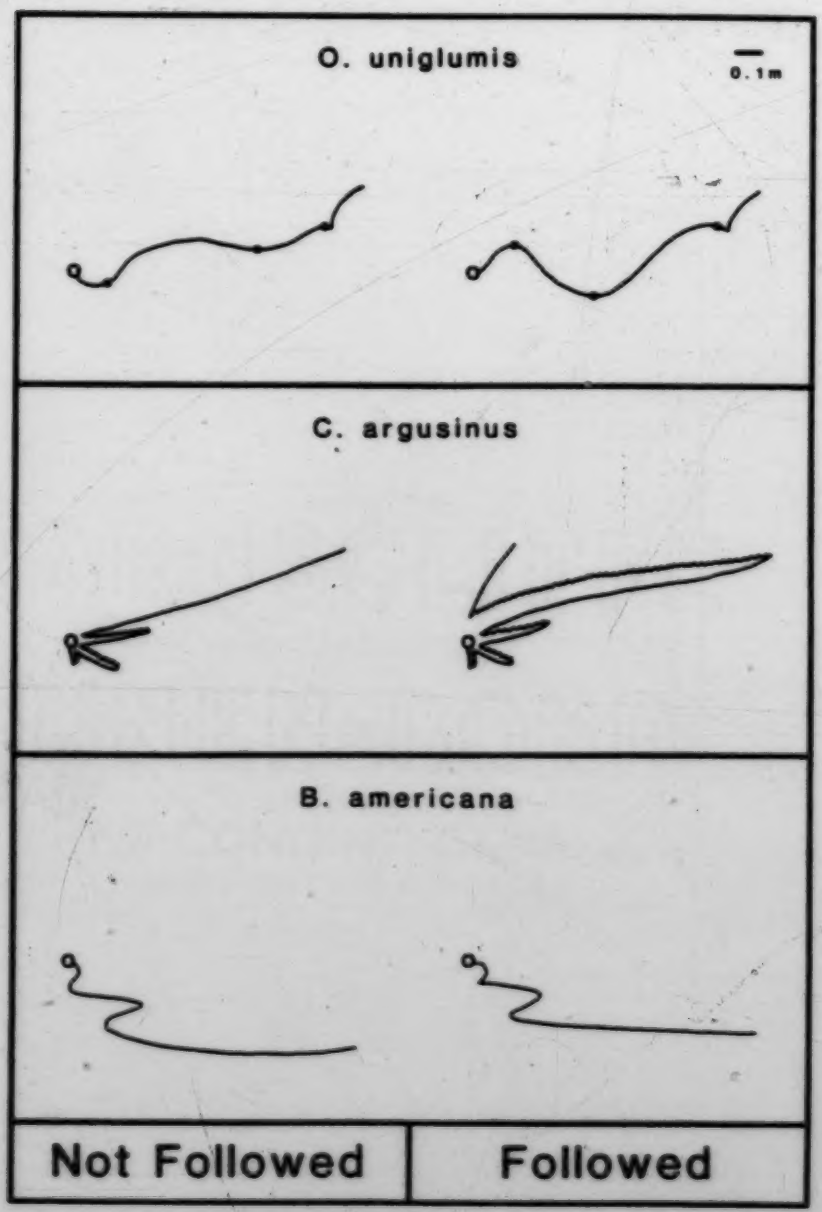
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Figure 8: The percentage of provisioning flights of female *Crabro argusinus*, *Bembix americana* and *Philanthus gibbosus* that were followed by *Senotainia trilineata* females at different times through the day.

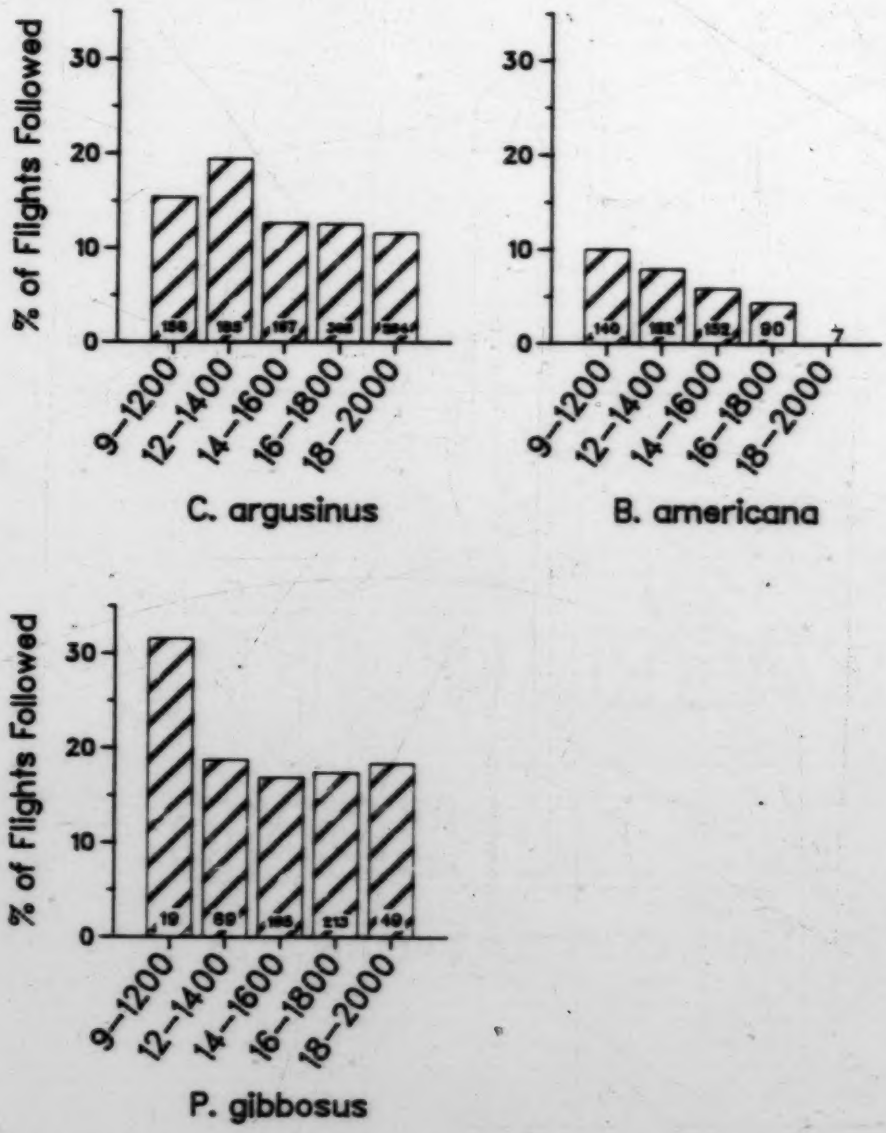


Figure 9: The number of zigzags performed during non-followed (N=147) and followed (N=95) provisioning flights by *Crabro argusinus* females.

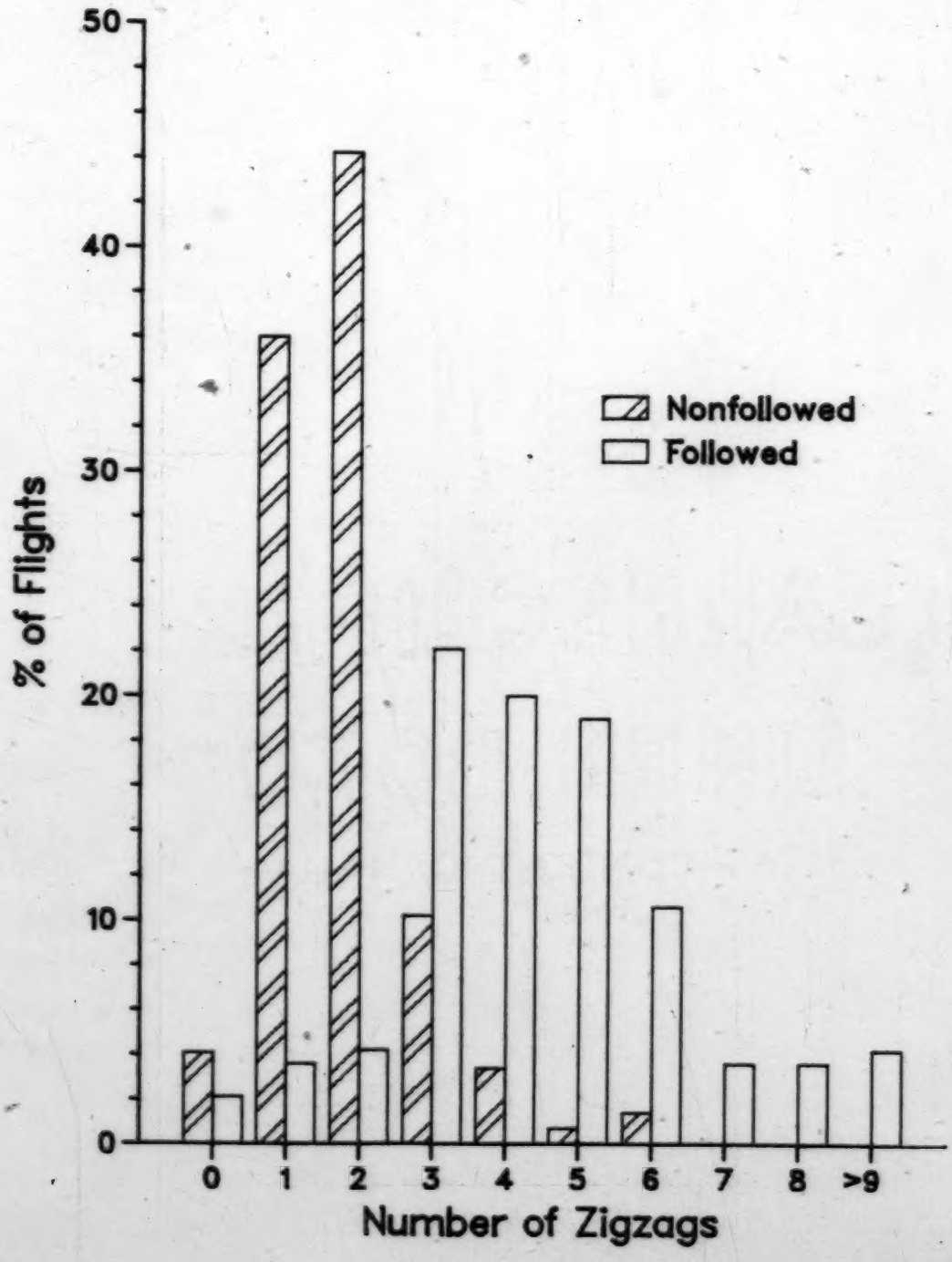


Figure 10: The lengths of zigzags performed during non-followed (N=260) and followed provisioning flights by female *Crabro argusinus* .

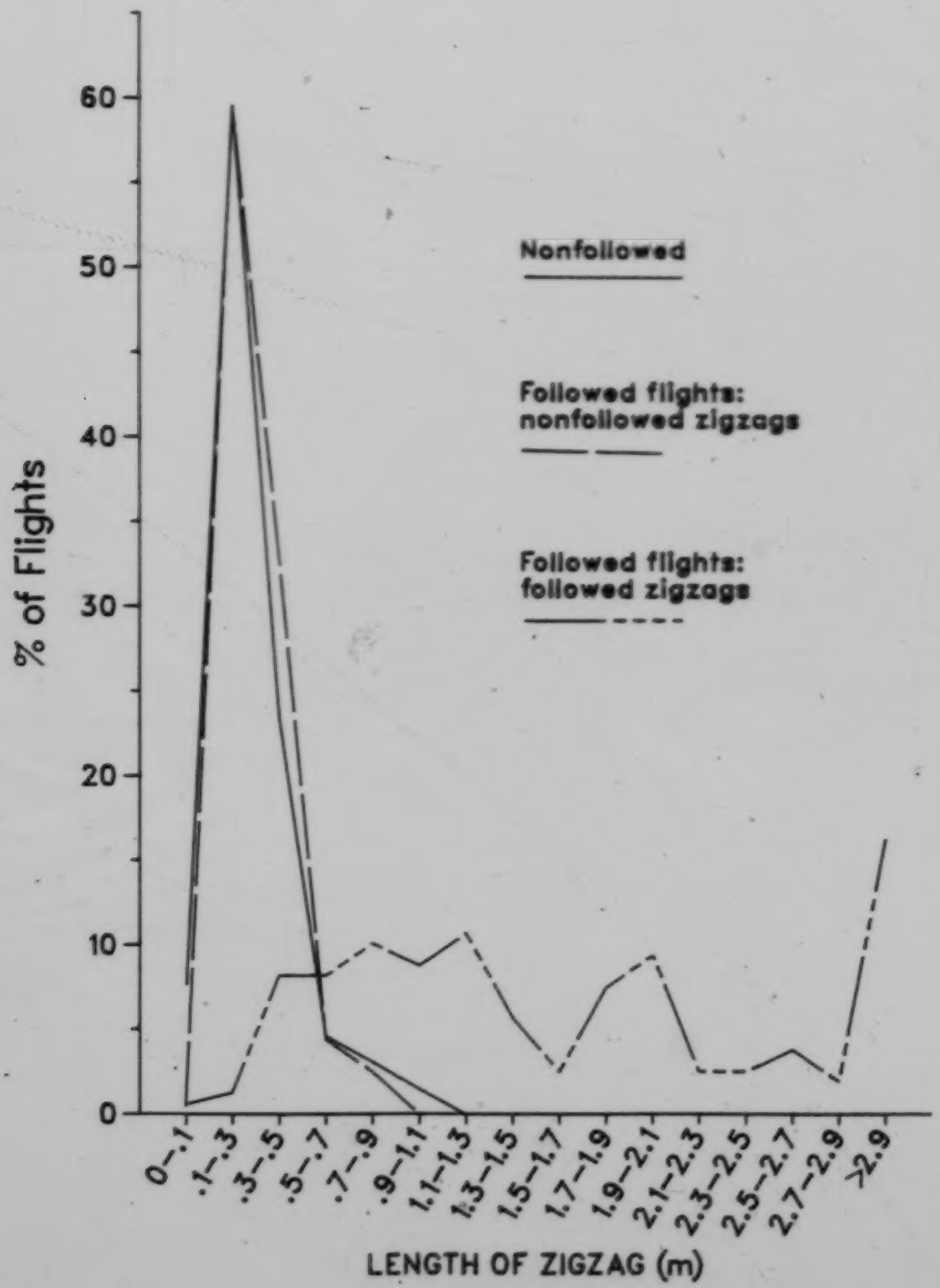


Figure 11: The maximum daily number of provisioning female *Philanthus gibbosus*, *P. inversus* and *Cerceris echo* during a ten day period beginning with the dates indicated on the X axis.

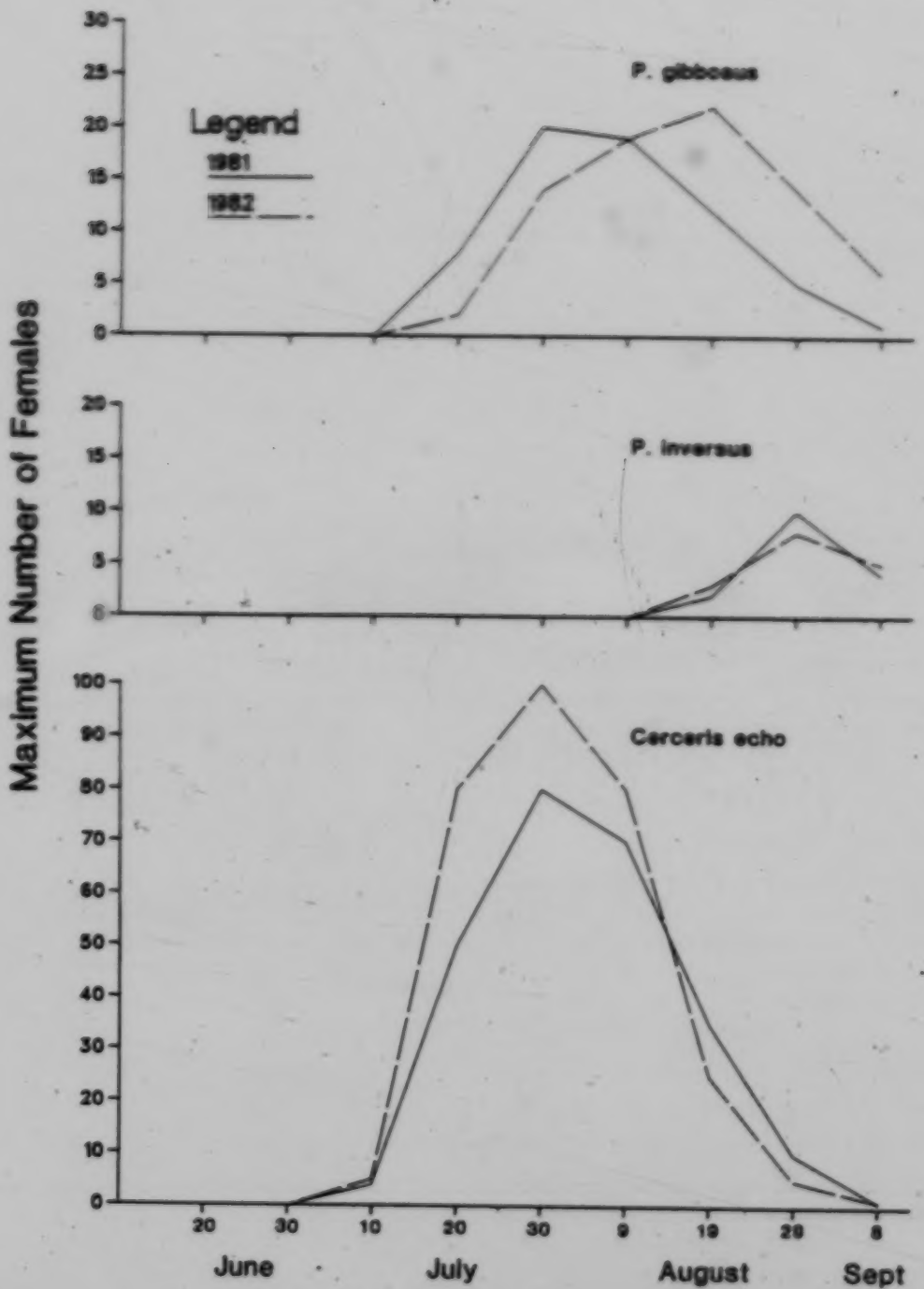


Figure 12: The typical pattern of provisioning flights of *Philanthus gibbosus*, *P. inversus* and *Cerceris echo* females.
o nest entrance. • wasp stationary.
----slow flight with abdominal waggle.

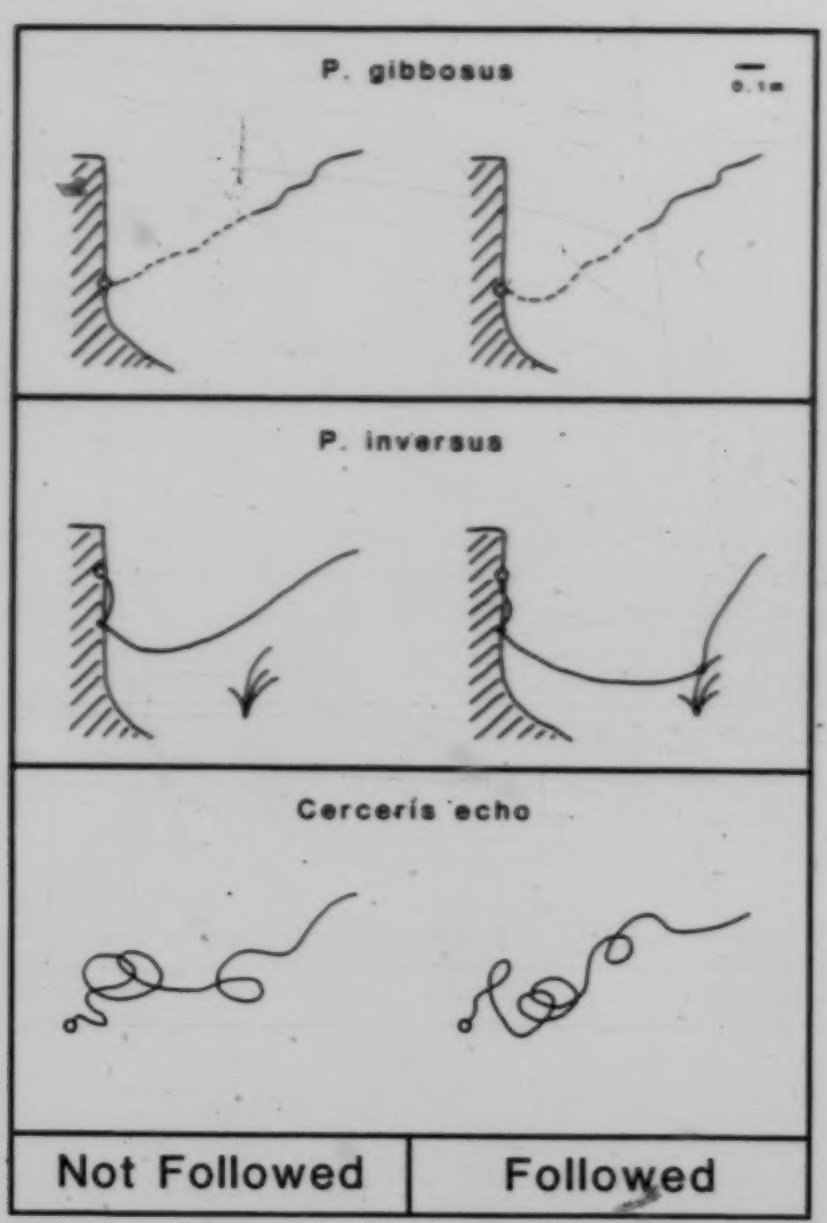


Plate 1: The study site in Writing-on-Stone Provincial Park; the flat portion of the sand scrape is in the centre, the slope and vertical panel to the left and the Milk River to the southeast in the background.

Plate 2: Two marked *Bembix americana* nests. The entrances are at 7:00 to the toothpicks.

Plate 3: Application of an individually identifiable mark to the thorax of a female *Cerceris echo*. In 1981, most wasps were anaesthetized while being marked, while in 1982 none were anaesthetized.

Plate 4: A marked female *Senotainia trilineata* (about 4mm long).

Plate 5: Female *Oxybelus uniglumis* carrying an anthomyiid fly on her sting. She is removing the temporary closure of her nest entrance with her front legs.

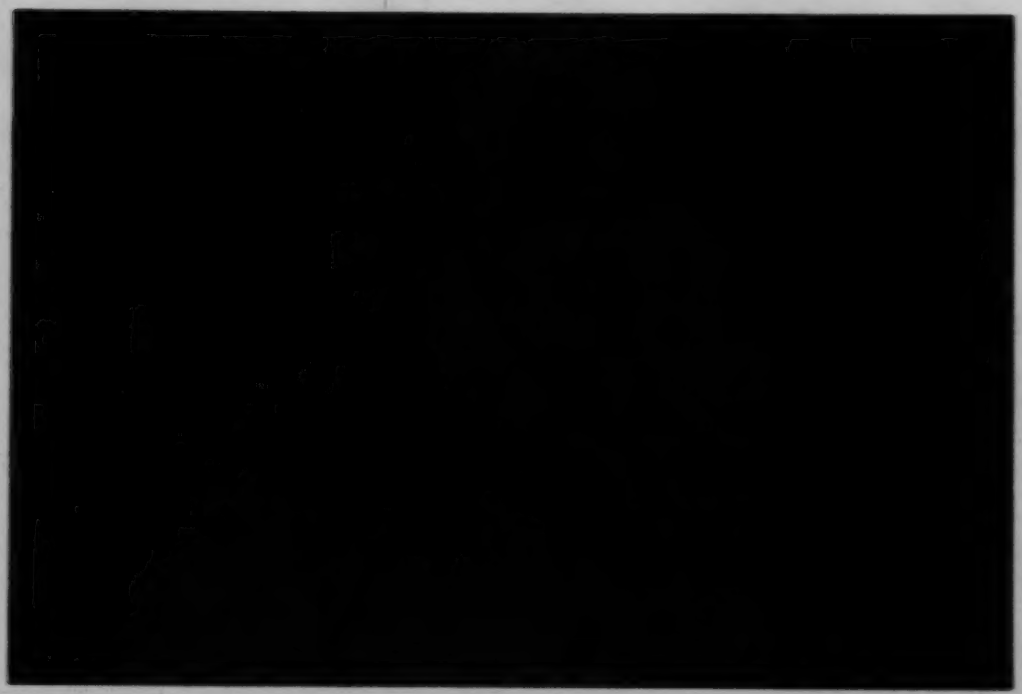
Plate 6: Female *Crabro argusinus* at her nest entrance, carrying a dolichopodid fly as prey.

Plate 7: Female *Bembix americana* entering her nest, with a bombyliid fly as prey. Note how the prey is exposed as the wasp enters the nest.

Plate 8: Female *Philanthus gibbosus* carrying an halictid bee. She has just landed; the covered nest entrance is directly below her mandibles.

Plate 9: Halictid bee taken from a female *Philanthus gibbosus* immediately after a female *Senotainia trilineata* contacted the bee. Note the four white *S. trilineata* maggots attached in a clump near the tip of the abdomen.

Plate 10: A female *Philanthus inversus* stopped within 0.5m of her nest. She is being watched by a female *Senotainia trilineata* sitting about 30cm behind her. The wasp is carrying a male *Agapostemon* bee.



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